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Rediscovery, Distribution and Phytogeographic Affinities of Leptogramma pilosa in Alabama

JOHN W. SHORT and JOHN D. FREEMAN*

Leptogramma pilosa var. *alabamensis* (Crawford) Wherry was originally described as *Thelypteris pilosa* var. *alabamensis*, based on material collected in Winston County, Alabama (Crawford, 1951). The type locality was stated to be a sandstone cliff on the "West Fork of the Sipsey River" five miles east of Double Springs (presumably where U.S. Highway 278 crosses Sipsey Fork[1]), at 400 m

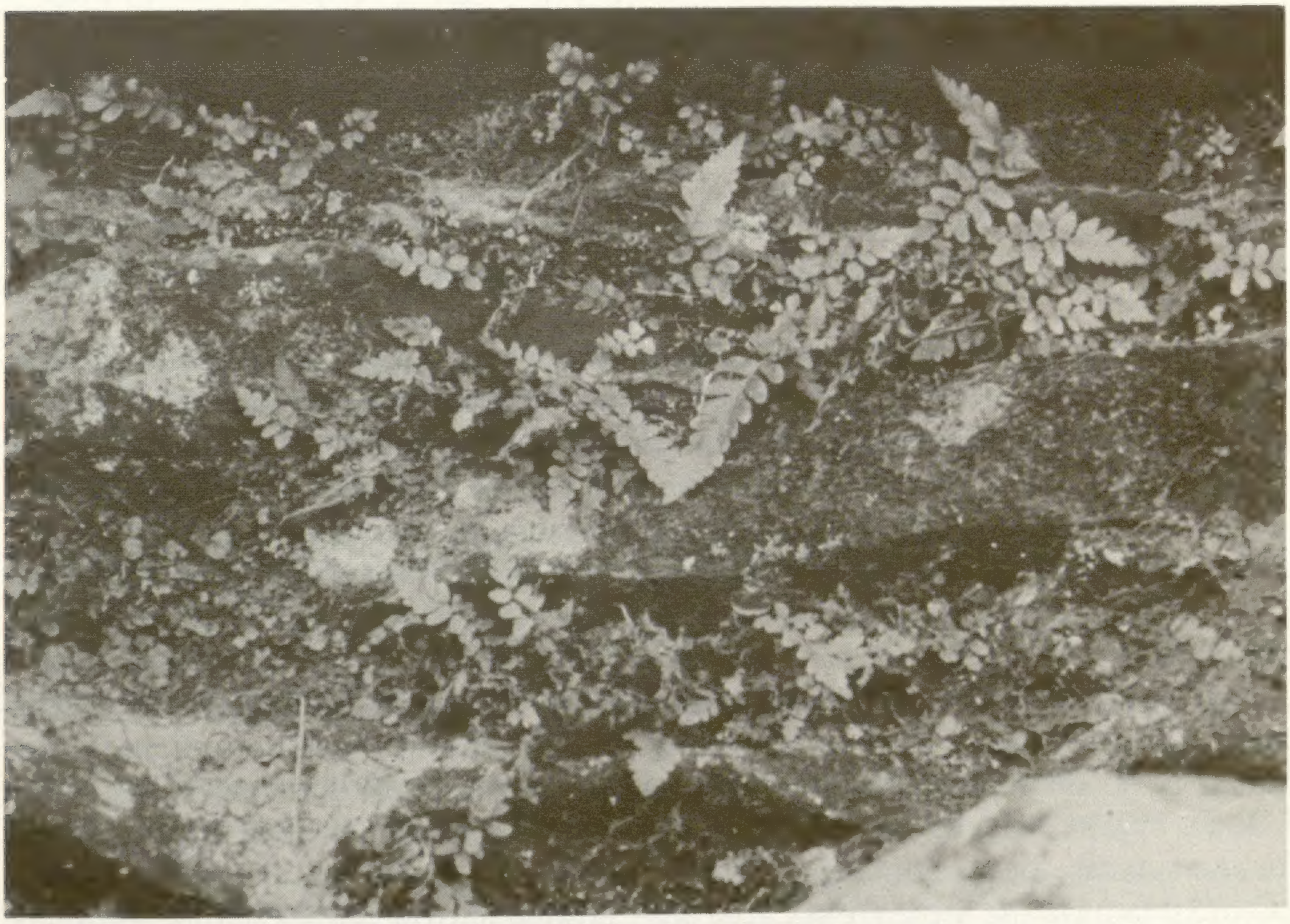

FIG. 1. Plants of *Leptogramma pilosa* var. *alabamensis*.

(1300 ft) elevation. Crawford identified two additional collections from the Mexican states of Chihuahua and Sonora as var. *alabamensis*, whereas the typical variety previously had been known from Chihuahua and central and southern Mexico and Guatemala. The species has not been reported until now from any locality in the United States other than the one cited by Crawford.

---

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[1]The nomenclature of the river at the collecting site is confused. On recent highway and topographic maps, it is called "Sipsey Fork." Colloquially it is called the "Sipsey River" or just "the Sipsey." The full and correct name perhaps should be "Sipsey Fork of the Black Warrior River."

Volume 67, number 4, of the JOURNAL was issued December 31, 1977.

In 1960, when the L. M. Smith Dam was completed several miles downstream from the type locality, the higher water level of Smith Lake in the Sipsey gorge necessitated construction of a new bridge for U.S. Highway 278. This construction leveled the cliff, and with the impoundment of Smith Lake completely destroyed the habitat in which *L. pilosa* var. *alabamensis* occurred. The species was assumed to have been lost from the Alabama (and, indeed, the U.S.) flora (Dean, 1969).

At a conference on rare and endangered species of Alabama held at Tuscaloosa in the spring of 1975, it was disclosed by Mrs. L. C. Smith (pers. comm. to J.D.F.) that *L. pilosa* had been observed somewhere along the Sipsey near the reported locality. Topographic maps revealed that a likely location would be the massive sandstone cliffs five miles *north* of Double Springs where Alabama Highway 33 crosses the river. Since no point in Winston County is more than 1,000 feet in elevation, it was clear that the elevation indicated by Crawford for the type locality had been in error.

In September 1975 and April 1976, several colonies of *L. pilosa* var. *alabamensis* were found near the Alabama Highway 33 bridge over Sipsey Fork, at the upper reaches of Smith Lake. This site is marked by an overhanging cliff rising more than 60 feet above the river. *Leptogramma pilosa* occurs in crevices in the north-facing cliff and on a smaller, west-facing cliff downstream *(Fig. 1)*. The thin, damp soil has been described as moderately acid (Wherry, 1964). The elevation of Smith Lake is about 500 feet; all colonies of *L. pilosa* observed were about 10 feet above water level and grew in close association with *Trichomanes boschianum* and various bryophytes. The type locality downstream was probably several feet lower. Other pteridophytes found nearby included: *Osmunda regalis, Athyrium asplenioides, A. thelypteroides, Woodwardia areolata* and *Selaginella apoda*.

Leptogramma pilosa still has not been found in the United States outside the gorge of Sipsey Fork. Besides the localities cited above, it has been seen in the Sipsey River Picnic Area near the Lawrence County line (R. Kral, pers. comm. to J.W.S., 1976). This gorge is over 1,200 miles from the nearest Mexican localities for the species. Located in the Cumberland Plateau just above the Fall Line, all major streams in the Sipsey Fork area have eroded narrow gorges with steep sides and many cliffs. These damp, cool gorges harbor a peculiar and unique assemblage of plant species including several near endemics as well as disjunct populations of species with principal ranges elsewhere. The Hemlock-Hardwood Forest Association is well developed in the gorges, some 150 miles from the southern limit of its main range in the Appalachian Mountains. *Trichomanes boschianum* and *T. petersii* are more abundant in these gorges than anywhere else. Whether the disjunctions in this area resulted from direct connections between floras or long range dispersals has not been determined.

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Chromosome Numbers in the Fern Genus Anogramma, II.

JUDITH G. BAROUTSIS* and GERALD J. GASTONY**,[1]

In an earlier report on chromosome numbers in the genus *Anogramma* (Gastony & Baroutsis, 1975), three new counts were established and all known previous counts were summarized. At that time, a count of $n=26$ for *A. leptophylla* from Europe (Kurita, 1971) was overlooked. We wish now to acknowledge this count, to report new counts made for populations of *A. guatemalensis* and *A. leptophylla*, and to suggest an explanation for some of the variant counts previously reported for *A. leptophylla*.

The general techniques for chromosome preparations were those previously discussed (Gastony & Baroutsis, 1975). To maximize chromosome staining, however, a propionic-iron-haemotoxylin stain (Henderson and Lu, 1968; Rigby, 1973) was applied to fixed mitotic cells of *Anogramma* gametophytes. The stained chromosomes were visually enhanced by use of phase microscopy in analysis and photographic work.

To promote spreading and separation of mitotic cells during squashing, material was treated with one of two preparations: Glusulase (Endo Laboratories Inc., Garden City, NY), a commercially available enzyme mixture from the intestinal juice of the snail *Helix pomatia*, was applied full strength to gametophyte tissue for four hours (Fabergé, 1945); Driselase (Kyowa Hakka Kogyo Co., Tokyo, Japan), a fungal-produced enzyme mixture, was applied as a 10% (w/v) aqueous solution according to the Glusulase schedule. Both preparations were equally satisfactory for softening cell walls. The potential of this enzyme technique in working with gametophyte chromosomes has been more fully discussed by Gastony (1977).

Chromosome counts for *A. guatemalensis*, published here for the first time, are based on three unequivocal counts. The counts reported for *A. leptophylla*, however, are based only on the material illustrated in *Figs. 3, 4, 8*, and *9*.

Sources of spores cultured to provide living material of the taxa herein reported are: *A. guatemalensis*, *Gastony 1037*, Depto. Chimaltenango, Guatemala; *A. leptophylla*, 7 Oct 1972, *Mickel*, Edo. Oaxaca, Mexico; *A. leptophylla*, 20 Oct 1972, *Esterhuysen*, Cape Province, South Africa. Voucher specimens of the plants raised from spores are deposited at IND.

RESULTS AND DISCUSSION

Mitotic squashes from gametophytes of *A. guatemalensis* and *A. leptophylla* show a chromosome number of $n=29$ (*Figs. 1-7*). Chromosomes of both these species have a strong tendency to stick together, particularly at their ends. This stickiness, in conjunction with the form of two of the chromosomes as discussed

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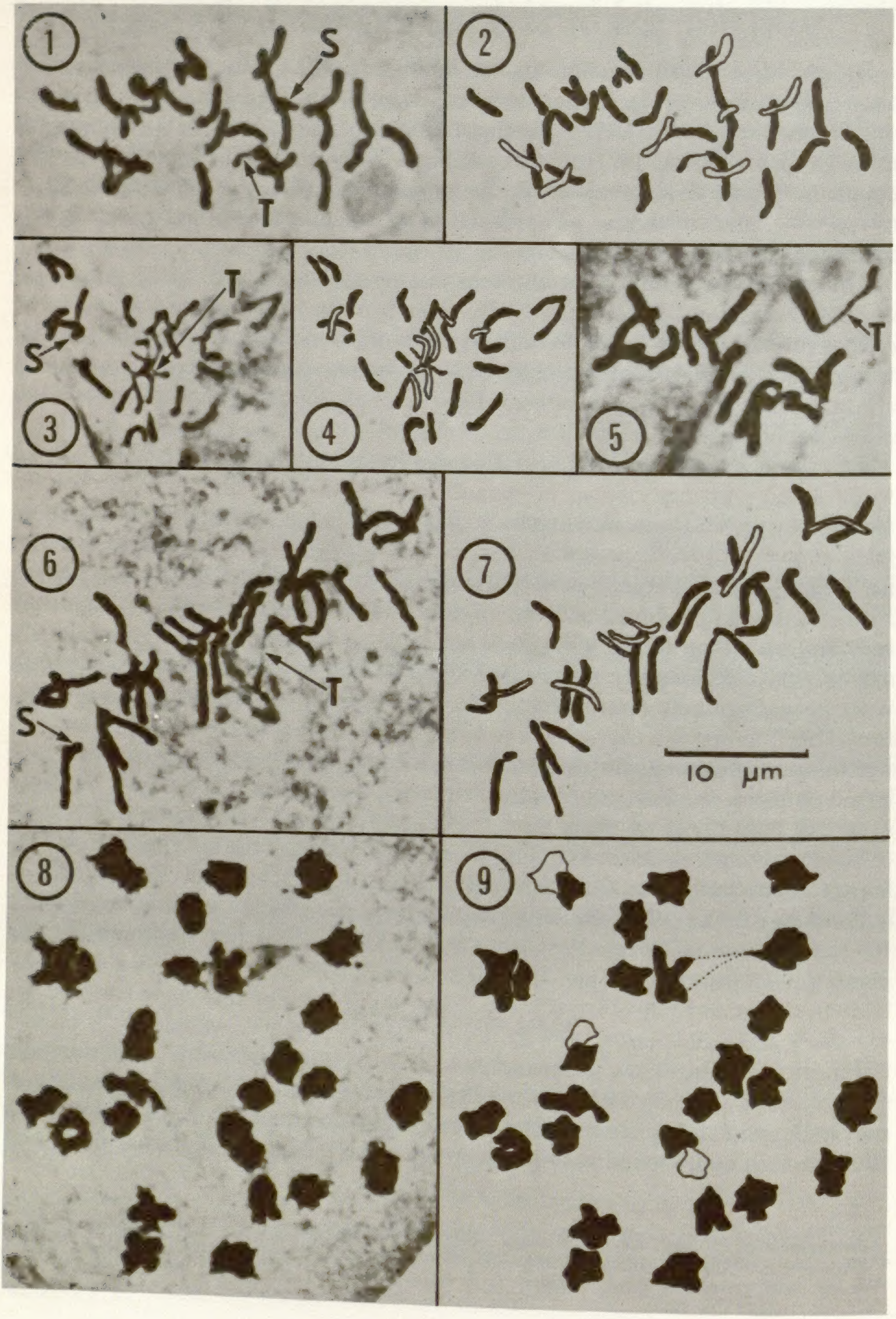
[1]We are most grateful to E. A. Schelpe, E. Esterhuysen, and J. T. Mickel for providing us with materials used in this study.


1
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6
S
T
7
10 µm
8
9

below, may explain the variability in the counts that have been reported for Mexican *A. leptophylla* (Mickel et al., 1966) and in at least some of the other previously reported counts which are at variance with a base number of 29.

An analysis of chromosome morphology in the course of this work has proven useful in ascertaining the actual chromosome numbers present and in determining the source of variability often encountered in *Anogramma* squashes. From observing numerous cells, it is known that both *A. leptophylla* and *A. guatemalensis* have one very thin chromosome (*Figs. 1, 3, 5,* and *6*) and a short chromosome that frequently appears as a knob at the end of another chromosome (*Figs. 1, 3,* and *6*). Prior to squashing, and often in squashed preparations, the short chromosome looks like a satellite. After squashing, however, it often lies at right angles to the chromosome with which it is associated (*Figs. 3* and *6*) or across this chromosome (*Fig. 1*). The thin chromosome also seems always to be associated with another chromosome, but in several cases it has been found completely free. The reason for these chromosomal associations is unknown. In at least half (ca. 10) of the cells examined, one or both of these chromosomes is not evident, and when counted, these cells appear to have 27 or 28 chromosomes.

As in mitotic preparations, meiotic squashes also reveal a tendency for chromosomes to stick to one another. The resultant difficulties were noted earlier (Gastony & Baroutsis, 1975) and were experienced again in attempts to count *A. leptophylla* from South Africa. Only one clear meiotic count of $n=29$ has been obtained from this South African material thus far (*Figs. 8* and *9*). The conditions causing chromosomal clumping thus appear to be present in both meiotic and mitotic cells.

The similarity in chromosomal morphology and behavior in gametophyte cells of *A. guatemalensis* and *A. leptophylla* parallels other shared features, such as identical spore morphology, similar gametophyte development, and similar physiological response to growth conditions (Baroutsis, 1976). Altogether, this evidence supports Tryon's (1962, p. 75) suggestion that *A. guatemalensis* may be an infra-specific variant of *A. leptophylla*. Final taxonomic disposition, of course, will require comparative morphological studies of populations throughout the North and Central American ranges of these two species.

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FIGS. 1-9. Photographs and camera lucida clarifications of *Anogramma* chromosomes of specimens cited in the text. FIGS. 1-7. Mitotic figures from gametophyte cells. FIGS. 8-9. Meiotic figure from spore mother cell. T = thin chromosome, S = short chromosome. FIGS. 1-2. *A. guatemalensis*, $n=29$. FIGS. 3-4. *A. leptophylla*, Mexico, $n=29$. FIG. 5. *A. guatemalensis*, portion of a squash included to show thin chromosome, T. FIGS. 6-7. *A. guatemalensis*, $n=29$. FIGS. 8-9. *A. leptophylla*, South Africa, $n=29$.

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Curtis Eugene Delchamps (1925-1977)

Curtis Eugene Delchamps was born March 3, 1925, in New Orleans, La., but grew up in Mobile, Ala. He studied chemistry at the University of Alabama, Pennsylvania State University, and West Virginia University where he received the Ph.D. degree. While still a student at the University of Alabama, he married Earsie Ward, who was also a chemistry major. He started teaching chemistry at the University of Miami, Miami, Florida, in 1955, and continued there until his death September 12, 1977, from a heart attack.

Gene had a life-long interest in nature, especially wild flowers, and became interested in photography as a means of studying plants. When he first moved to Florida, he started to learn about the plant life there, both native and cultivated. He soon discovered that the local plant experts knew very little about the native ferns. Learning about them was a challenge to him, and he worked very hard on the group and soon became an authority in the field. He combined his plant expertise with his photographic skills, and became a popular lecturer on ferns.

He served for two terms as president of the Miami Men's Garden Club, and helped to bring national recognition to the group by sponsoring a successful candidate for the Johnny Appleseed Conservation award. He was first president of the South Florida Fern Society in Miami, and continued to serve on its Board of Directors until his death.

Perhaps Gene's greatest contribution to the world of ferns was his enthusiasm for learning and his eagerness to share his knowledge with others. This he did by organizing and conducting field trips, setting up study groups, giving numerous talks to garden clubs, and contributing educational articles for the club newsletters.

He is survived by his wife, Earsie, a daughter, Barbara, and a son, Charles-

Mrs. C. E. Delchamps, 18240 S.W. 248th St., Homestead, FL 33031.

Geographical Distribution of Isoëtes butleri in the Southeastern United States

JERRY M. BASKIN and CAROL C. BASKIN*

According to Pfeiffer (1922), *Isoëtes butleri* Engelm. occurs in Tennessee, Missouri, eastern Kansas and south into Arkansas and Oklahoma. In Tennessee, *I. butleri* is restricted to cedar (limestone) glades of the Central Basin, where the soil is water-logged during winter and early spring but may be extremely dry during late spring, summer, and autumn. The University of Tennessee and Vanderbilt herbaria have specimens of *I. butleri* from Bedford, Davidson, Maury, Rutherford, Williamson, and Wilson Counties. In addition, we have found the species in Marshall County on 7 May 1977, along State Road 99, 6.5 miles west of U.S. highway 31A (*J. & C. Baskin 1895,* VDB). All of the above collections were from cedar glades.

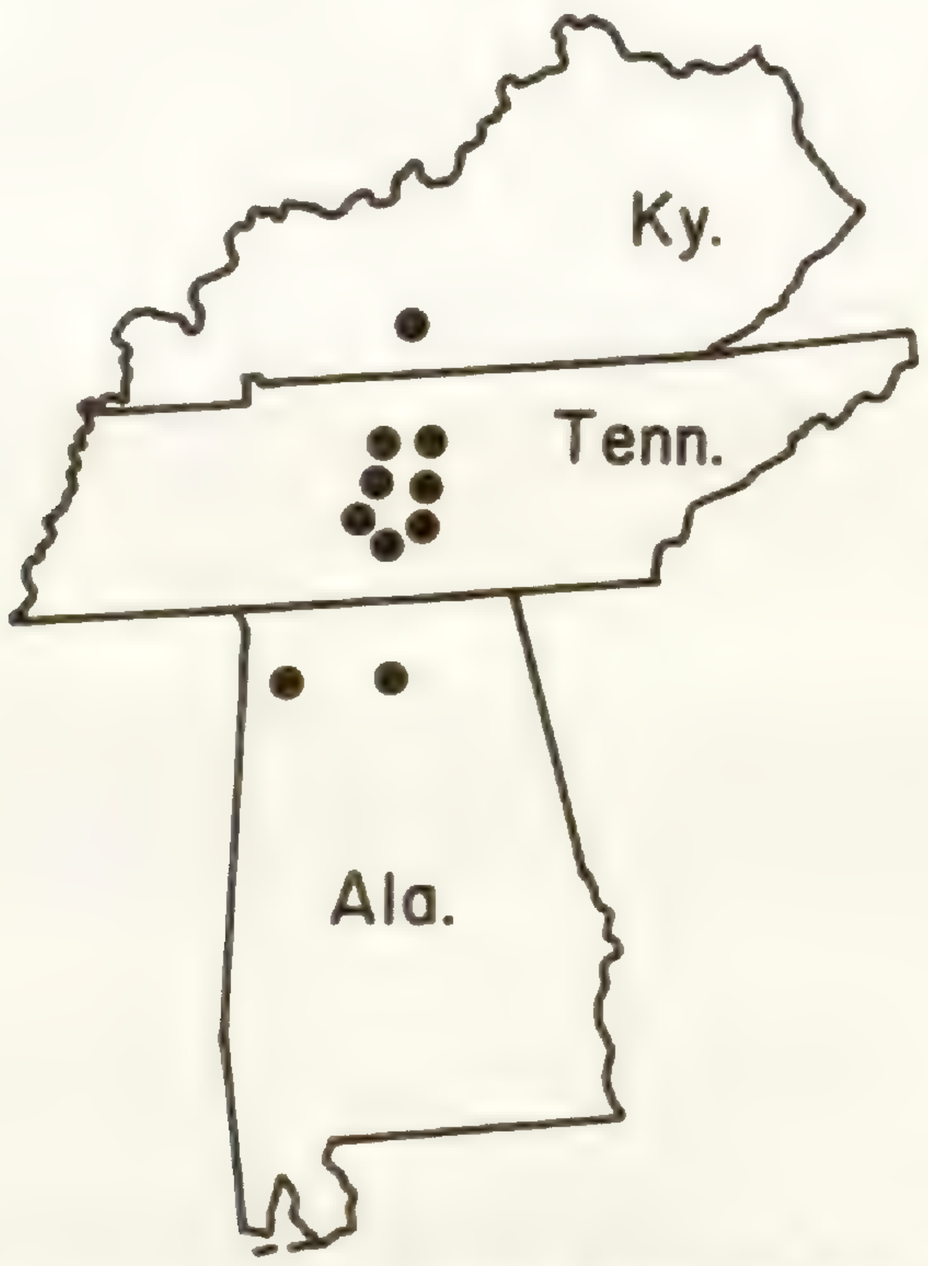

FIG. 1. A county dot distribution map of *Isoëtes butleri* in the southeastern United States.

Cedar glades also occur in northern Alabama and in Kentucky, but there has been only one previous report of *I. butleri* in Alabama, and the species has not been reported from Kentucky. The only report of *I. butleri* from Alabama is by Kral (1973), who collected the species on a limestone glade near Isbel in Franklin County. We have collected the species on a second cedar glade in Franklin County on 27 May 1977, east of Russellville along County Road 83, 0.6 miles north of State Road 24 (*J. & C. Baskin 1324,* VDB), and on a cedar glade in Morgan County on 6 Apr 1972, near McKendry, along Cedar Plains Church Road, 0.2 miles north of County Road 55 (*J. & C. Baskin 1193*, VDB). In Ken-

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tucky we have collected *I. butleri* on a cedar glade in Warren County on 12 Apr 1973, east of U.S. Road 31W, 0.2 miles north of the Warren-Simpson County line (*J. & C. Baskin 1648*, MIL, TENN, VDB). The presently known geographical distribution of *I. butleri* in southeastern United States is shown in *Fig. 1*.

In the southeastern United States, *I. butleri* has been collected only from calcareous glades. In a recent study of *Isoëtes* specimens from Arkansas, Missouri and Illinois, Taylor, Mohlenbrock, and Murphy (1975) concluded that *I. butleri* ". . . shows a definite affinity for drier upland sites, but more often calcareous, rather than sandstone ones." In his paper entitled "Some Features of the Flora of the Ozark Region in Missouri," Steyermark (1934) lists *I. butleri* as a typical calciphile. However, in his "Flora of Missouri," Steyermark (1963, p. 11) says that the species ". . . occurs both on sandstone and chert as well as on limestone glades." While discussing the occurrence of *I. butleri* on sandstone with the senior author, Dr. W. Carl Taylor said that some of the sandstones in the Ozark Region of Missouri are cemented together with calcareous material and that *I. butleri* growing on them may, in fact, be growing on a calcareous substrate.

We thank Dr. W. Carl Taylor of the Milwaukee Public Museum for verifying the identification of our specimens from Warren County, Kentucky.

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Thelypteris oroniensis, a New Species from Costa Rica

LUIS D. GÓMEZ P.*

The genus *Thelypteris* is one of the largest and most homogeneous of tropical ferns. Morphologically, it forms a very natural group, such as that of *Elaphoglossum*. Over 80 species of *Thelypteris* are known from Costa Rica, and yet recently a new species has been discovered on the isolated summits of the coastal hills facing the Caribbean, which is here described as:

Thelypteris oroniensis L. D. Gómez, sp. nov. **Fig. 1.**

Herba terrestris, rhizomate suberecto, lignoso, paucissime squamoso vel quasi glabro, squamis ample-latissimis, ambarinis, clathratis, stipitibus fasciculatis, stramineis, canaliculatis, pilis 1-cellulatis et stellatis dispersis. Frondes pinnatae, pinnis retroflexis, 7 paribus alternibus, rachibus flexuosis, pinnis basalibus sessilibus vel subsessilibus, venis utrinque 7-9 paribus per segmento. Indusium nullum.

Herbaceous, terrestrial plants with suberect rhizome 1.5-2 cm thick, woody, with a few amber brown, wide, clathrate scales. Stipes fasciculate, stramineous, 21-25 cm long, 2.5 mm in diameter, below with a few paleae, above glabrous, canaliculate, above with 1-celled and stellate hairs mixed. Fronds pinnate, with 7 pairs of alternate, retroflexed pinnae, the apical pinna conform, often with a long, adnate basal segment; fronds lanceolate in outline, truncate at the base, 40-45 cm long, 25-27 cm wide, papyraceous, green above, glaucous-greenish underneath, both surfaces glabrous. Rachis flexuose, helicoidal in growth, with mixed 1-celled and stellate hairs. Basal pinnae subsessile; middle pinnae and upper pinnae sessile. Pinnae 11-15 cm long, 2.5-3.7 cm wide, elongate-lanceolate, the apex narrowly acuminate, with 21 pairs of segments, some often lacking and reduced to a narrow wing, the basal pinnules unequal, the upper ones reduced or even absent, the lower ones auriculate, broad, and overlapping the rachis. Veins 7-9 pairs per segment. Sori medial; indusia absent. Sporangia with acicular hairs on the walls and stalks. Many spores aborted.

HOLOTYPE: Monte Oroni (Chase 27), lower Talamanca, Pcia. Limón, Costa Rica, *Ocampo 1635* (CR 64453; isotypes UC, US).

Thelypteris oroniensis resembles *T. nicaraguensis* (Fourn.) Morton in habit and pinna shape, but differs from it and other species of subg. *Goniopteris* by its flexuose rachises and helicoidal growth of the plants. Among the New World species of *Thelypteris*, only one Ecuadorian species of subg. *Amauropelta* has flexuose rachises.

*Herbario Nacional, Museo Nacional de Costa Rica, Apartado 749, San José, Costa Rica.

FIG. 1. Holotype of Thelypteris oroniensis, *Ocampo 1635* (CR).

Additions and Corrections to the Pteridophyte Flora of Chihuahua, Mexico

IRVING W. KNOBLOCH* and DONOVAN S. CORRELL**

Since the publication in 1962 of our "Ferns and Fern Allies of Chihuahua, Mexico," several additional species have been found in the State. Also, some changes and corrections have been noted that should be made available to others.

ADDITIONS AND DELETIONS

1. Selaginella mutica D. C. Eaton var. mutica

Vicinity of Cerro Bola, Sierra del Paso del Norte (Juarez Mts.), on edge of the city of Juarez, *Knobloch 2110* (MSC). This specimen was verified by Rolla M. Tryon, Jr. This addition, which is also new to Mexico, was reported by Knobloch (Amer. Fern J. **56:** 36. 1966). In the same publication, new stations in Chihuahua were reported for *S. pallescens* (Presl) Spring and *S. rupincola* Underw.

2. Anemia tomentosa var. mexicana (Presl) Mickel

As a result of John Mickel's work on the genus, we now add this taxon to our flora and eliminate *A. anthriscifolia* Schrad. The latter, according to a personal communication from Mickel, does not occur in Mexico. All specimens cited in our manual are to be referred to *A. tomentosa* var. *mexicana*.

3. Asplenium sessilifolium Desv.

Reported from canyon below Basaseachic Falls by Timothy Reeves (Amer. Fern. **67:** 62. 1977).

4. Bommeria subpaleacea Maxon

According to C. Haufler (pers. comm.), *B. knoblochii* Maxon, which we cited as a valid species, is a synonym of *B. subpaleacea* Maxon (Contr. U.S. Natl. Herb. **17:** 169. 1913).

5. Plagiogyria pectinata (Liebm.) Lellinger

All of the specimens cited in our work as *P. semicordata* (Presl) Christ should be referred to this species. According to Lellinger (Amer. Fern J. **61:** 110-118. 1971), *P. semicordata* does not occur in northern Mexico.

6. Pteris cretica L.

Reported from the canyon below Basaseachic Falls by Timothy Reeves (Amer. Fern J. **67:** 62. 1977).

7. Thelypteris puberula var. sonorensis A. Reid Smith

Since var. *puberula* is not considered to occur in Chihuahua, all specimens in our manual should be referred to the var. *sonorensis*.

8. Thelypteris ovata var. lindheimeri (C. Chr.) A. Reid Smith

Santa Elena Canyon region in the extreme northeastern part of Chihuahua, *Brenckle & Koch 51032* (US), cited by Smith (Univ. Calif. Publ. Bot. **59:** 118. 1971).

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9. Thelypteris resinifera (Desv.) Proctor

La Bufa, southeast of Creel, *Knobloch 579* (MSC). This previously unidentified specimen is referrable to this species, according to a personal communication from A. R. Smith.

CORRECTIONS

Page 5, line 21: or Short-thorn Forest.
Page 17: *Psilotum nudum* (L.) Beauv.; *Anemia tomentosa* var. *mexicana*.
Page 34, line 5: omit Pl. 6.
Page 35: *Equisetum laevigatum=E.* × *ferrissii* Clute.
Page 36, line 34: after "ferns" add "and allies."
Page 46, line 26: *Anemia anthriscifolia=A. tomentosa* var. *mexicana* (Presl) Mickel, Iowa State J. Sci. **36:** 427. 1962.
Page 78, line 15: add Baja California.
Page 78, line 34: add Baja California.
Page 85, line 24: for "*Knobloch 584*" read "*Knobloch 449*."
Page 85, line 41: for "bipinnate-pinnatifid" read "tripinnatifid."
Page 87, line 6: add Arkansas.
Page 93, line 32: add Missouri.
Page 97, line 33: add Sonora.
Page 100, last line: add Hidalgo.
Page 102, line 1: *Cheilanthes meifolia* is now referred to *Aspidotis meifolia* (D. C. Eaton) Pic.-Ser., Webbia **7:** 327. 1950.
Page 104, line 7: add Guanajuato, Jalisco, and Durango.
Page 104, line 26: delete "*Knobloch 449*."
Page 105, line 16: after "glabrous" add "occasionally hairy."
Page 151, line 2 from bottom: add North Carolina.
Page 180, line 4 from bottom: "Chihuahua," not "Chuhuahua."
Page 184, line 5: "Segorachi" not "Sugorachi."

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The Distribution and Chemical Constituents of the Farinose Exudates in Gymnogrammoid Ferns

ECKHARD WOLLENWEBER*

Many members of the Polypodiaceae *sensu lato* show a conspicuous, yellow or white deposit on the lower surface of their fronds. Therefore, they are often called gold ferns, gold-back ferns, silver ferns, or silver-back ferns. This is especially true for members of the genus *Pityrogramma* Link. Such deposits also occur in *Cheilanthes* Swartz and *Notholaena* R. Br., although they are less known because species of these genera are not easily cultivated in greenhouses. The culture of the decorative species of *Pityrogramma* was especially in fashion at the beginning of the 19th century. Both *P. calomelanos* (L.) Link and *P. chrysophylla* (Swartz) Link were grown at Kew beginning in 1790. Fanciers were attracted by the great variability of species and strains and by the formation of various forms and hybrids that occurred during the culture of "*Gymnogramma*." However, the proliferation of hybrids and horticultural forms led to serious taxonomic confusion. Domin's (1929) statement is still valid: one can easily find completely different species or hybrids grown in greenhouses under the same name. Even recently in botanical gardens the name *P. sulphurea* (Swartz) Maxon has been applied to varieties of *P. chrysophylla* and *P. austroamericana* Domin.

ANATOMICAL OBSERVATIONS

The special anatomical features of the gymnogrammoid ferns were described rather early. Schkuhr (1804, p. 4, *t. 4*) reported that the lower surface of the fronds of the Schwefelgelber Vollfarn, now *Adiantum poiretii* var. *sulphureum* (Kaulf.) Tryon, were covered with an amorphous, yellow web. We owe to Schkuhr charming drawings of entire plants. As to my knowledge, the first detailed figures showing stalked glands themselves were published by Link (1842, *t. III, figs. 7-9*). De Bary (1877, p. 105) gave a good description of farina-dusted capitate hairs, or "pili pulverulenti" as he called them. The farinose coating of these plants is not excreted by the entire epidermis, like a true wax coating, but is formed exclusively by the globose terminal cell of small hairs which have a short, unicellular stalk. The wax is exuded on the whole surface of the terminal cells in the shape of rod- or needle-like crystals. Weatherby (1920) also has clearly described the glands and farina of *Pityrogramma triangularis* (Kaulf.) Maxon. A description similar to that of De Bary (1877, p. 105) was given by Nayar (1962) for *Cheilanthes:* "This large terminal cell secretes the waxy substance which appears like minute rods which are radially placed around the cell. On older stipes the hairs wither and the rods break up to form a powdery mass." De Bary (1877, p. 105) also published a drawing of such a capitate gland which is so far unsurpassed, showing the excreted material (*Fig. 1*). This figure has been copied by many authors, including Blasdale (1893). Comparatively less clear is the drawing by Höhlke (1902), which

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was copied even by Ogura (1972, p. 130). Höhlke stated that the cuticle was not lifted by the formation of secretions. He asserted that the exudate was formed in the "cell membrane" (i.e., cell wall) and he believed he saw pores in which the cuticle had been penetrated by the rods of exudate. Further drawings were published by Molisch (1923, p. 128), Bower (1923, p. 186), Dous (1927), and Nayar (1964). A small microphotograph was published by Smith et al. (1971). It should be noted here that epidermal waxes may form very similar filaments, as shown for example by Gunning and Steer (1977, *t. 9a, b*).

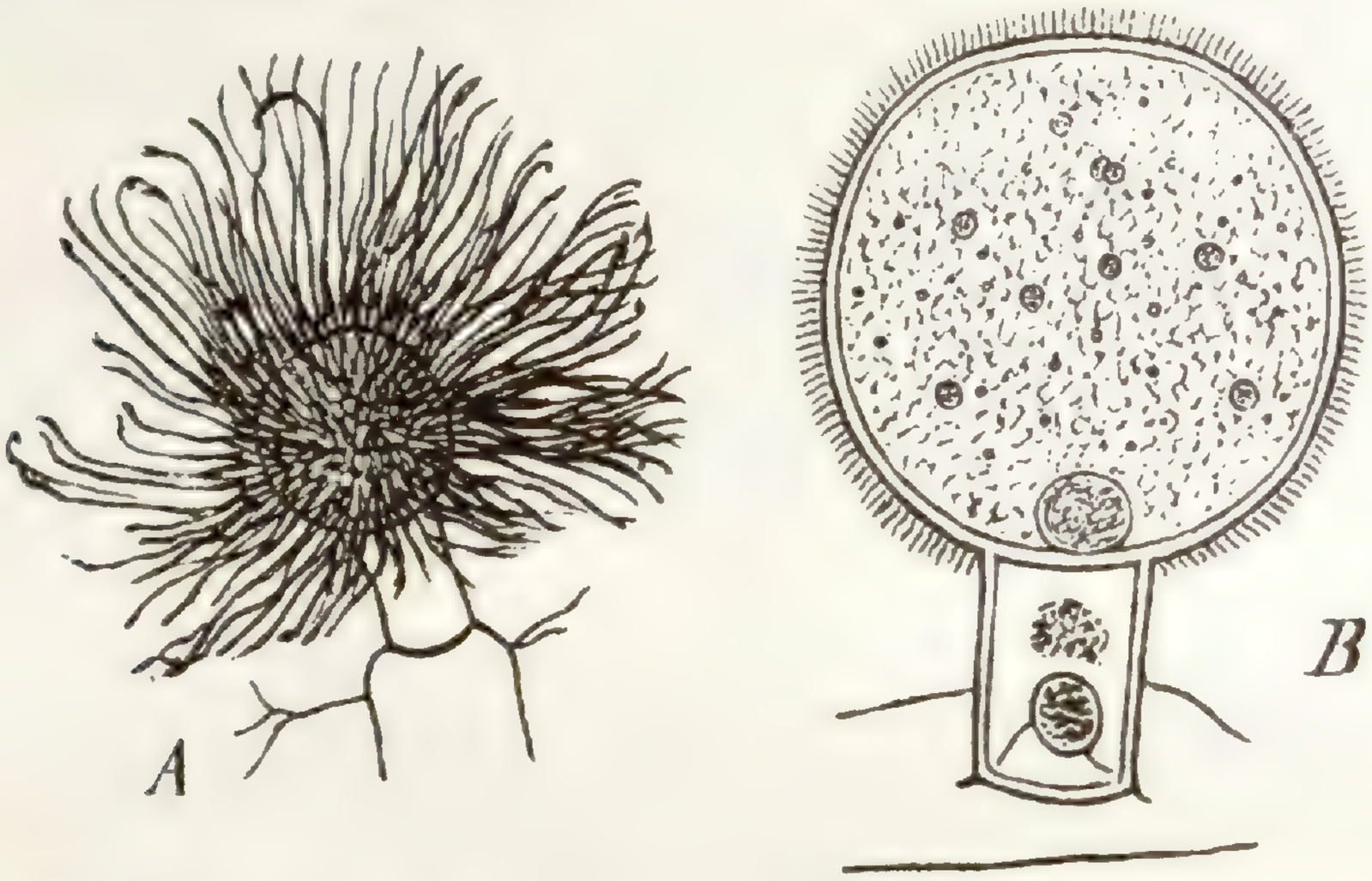


FIG. 1. Pili pulverulenti of *Pityrogramma tartarea* (B rinsed with alcohol), after De Bary (1877).

There has been only one investigation of the ultrastructure of exudate-secreting glands. Schnepf and Klasova (1973) studied the glands of *Pityrogramma chrysoconia* (Desv.) Maxon by transmission electron microscopy. They belong to the group of glands with a tubular, smooth endoplasmic reticulum as the dominant cell component; this means they are similar to those excreting volatile oils. The plastids seem to be involved in the formation of the flavonoids, but there is no proof of their accumulation in the vacuole. The flavonoids penetrate the cuticle and crystallize on its surface. These results resemble those obtained from the glands of *Primula* by Wollenweber and Schnepf (1970), which are likewise regarded as merocrinic glands by Lüttge and Schnepf (1976). The value of the single investigation by scanning electron microscopy (Guervin et al., 1971, on *Gymnogramma sulphurea* Desv.) is diminished because the authors illustrate and discuss the structure of a "cupula," which obviously is an artifact caused by shrinking of the capitate cell during fixation.

The location of the secretory glands varies. Farinose coatings usually are developed on the lower surface of fronds, but in some species they may appear, although less pronounced, on the upper surface, as in *Notholaena aliena* Maxon, *N. grayi* Davenp., *N. leonina* Maxon, *N. rosei* Maxon, *N. schaffneri* (Fourn.) Underw., and some others, according to Tryon (1956). Sometimes farina on the upper surface appears only in dots produced by isolated glands, as can be ob-

served on young fronds of *Pityrogramma austroamericana (Fig. 2).* Occasionally farina is produced abundantly on the rachis, mainly at its base, as in *Cheilanthes farinosa* (Forsk.) Kaulf., *P. calomelanos,* and *P. chrysophylla.* Blasdale (1877) stated, "Though normally occuring on the lower surface only they may appear on the upper, and in all cases they are distributed quite uniformly, that is, without reference to the sori, veinlets or other organs." However, in some species only the fertile pinnules have farinose coatings, as in *Onychium siliculosum* (Desv.) C. Chr. In *Pityrogramma trifoliata* (L.) Tryon, very young fronds bear sporadic patches of farina that soon disappear, and the fertile pinnae also have a farinose coating. In *P. calomelanos* I observed glands on the primary fronds, and according to Bower (1923, p. 199), they appear on the prothallia of *Notholaena trichomanoides* (L.) Desv.

Commonly either hairs and scales or a farinose coating—but not both—occur on the laminae of a single species, but exceptions are found in *Notholaena.*

In *N. aschenborniana* Klotzsch and *N. galeottii* Fée, the wax-like indument can be completely covered by scales. On the other hand, in *Cheilanthes* the separation into genera of the two sections *Cheilanthes* and *Aleuritopteris* Fée, as supported by some authors, is possible only because the two indument types exclude each other.

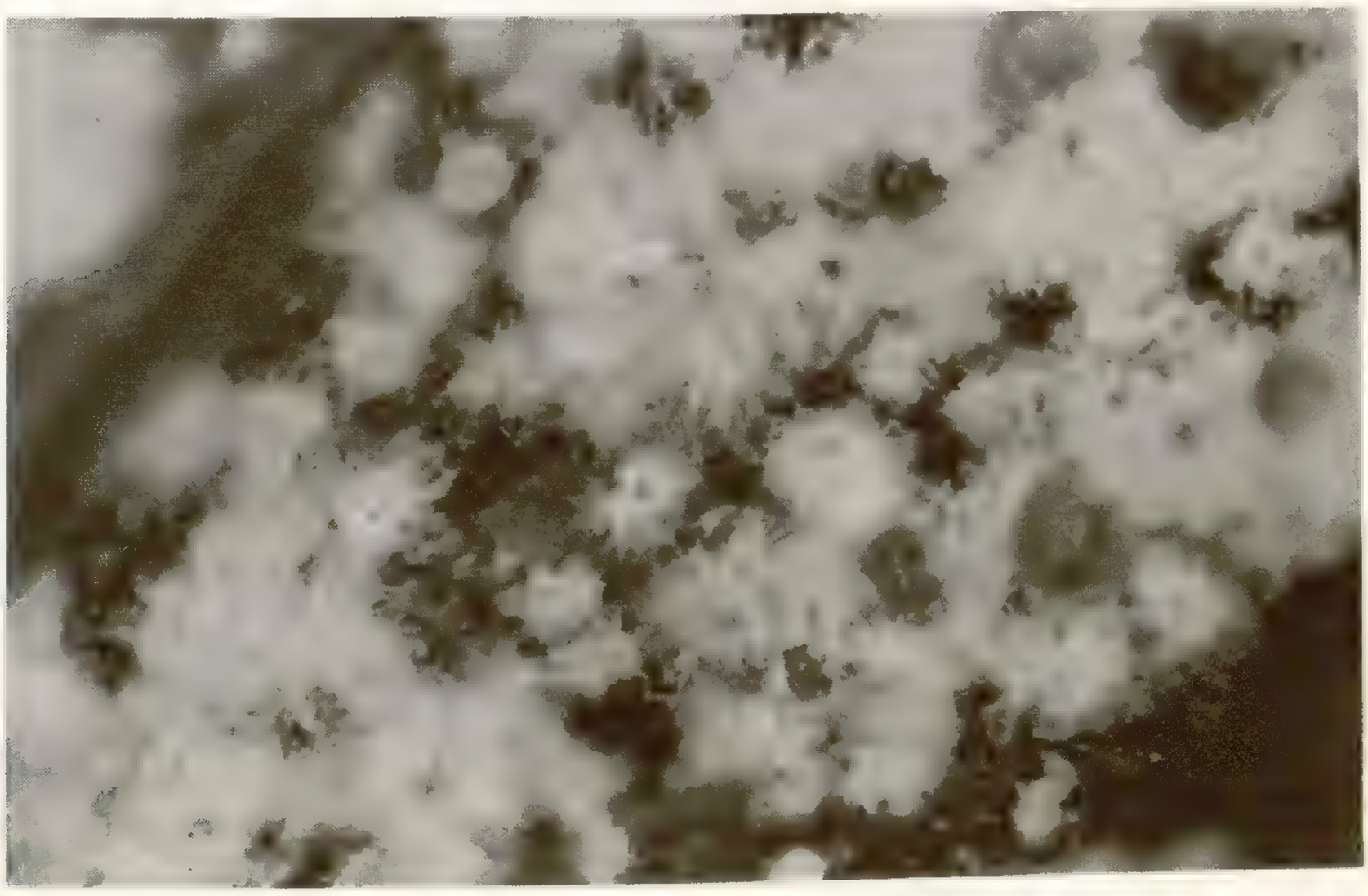


FIG. 2. Farina glands on a young frond of *Pityrogramma austroamericana.*

CHEMICAL NATURE OF EXUDATES

De Bary (1877, p. 105) was probably the first to distinguish farinose coatings ("mehlige Überzüge") from wax coatings. However, the material excreted by gymnogrammoid ferns was usually regarded as a wax-like substance up to the middle of the last century. In 1844, Göppert called it a resin, according to Wiesner (1876, p. 236). Klotzsch (1851) introduced the term "pseudo-stearoptenes" for a chemically undefined group of compounds he characterized as "parts of volatile

oils and resins condensed by heat withdrawal." He assumed that these compounds contain oxygen and counted among them coumarin from *Melilotus officinalis* and "Primula camphor" from *Primula auricula*. Wollenweber (1974) has shown the latter to be a mixture of various flavones, and therefore Klotzsch came rather close to the truth. On the other hand, he erroneously stated that excretion of the dry, farinose mass of fern fronds occurs without glands. Wiesner (1876) called the coatings of ferns "crystalline efflorescences," which he distinguished from plant waxes. The chemical classification of the substances, which were not precisely defined at that time, followed their solubility in water, alcohol, ether, and other solvents. From such investigations, Göppert derived his opinion that the yellow coatings of what is now called *Pityrogramma chrysophylla* are related to resins. This opinion was also expressed by Höhlke (1902). Christ (1897) used the terms "wax flour," "wax powder," or "farina" ("Mehl"), whereas Strasburger (1905, p. 87) called the exudate a "greasy substance." Haberlandt (1918, p. 477) mentioned the capitate hairs of *Gymnogramma* in a chapter dealing with oil, resin, slime, and gum glands. Möbius (1927, p. 152) compared the farinose coatings with wax exudates, Wetzel in Verdoorn (1938, p. 360) classified them with volatile oils as "resinous substances," and even Ogura (1972, p. 126) mentioned "fatty or resinous excretions."

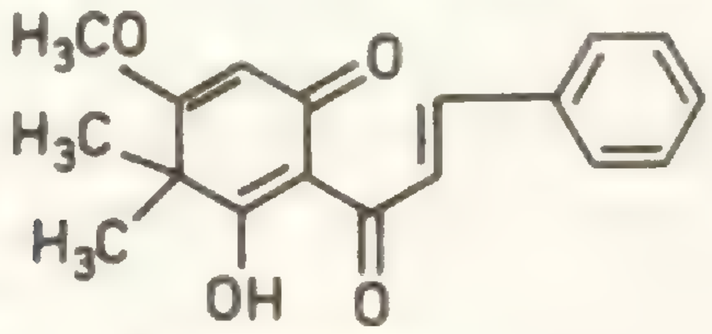
Under these circumstances, it is understandable that taxonomists even at the present time speak of "ceraceous ferns" and of "wax" in keys and descriptions. Apparently the results of recent chemical investigations published in chemical journals have not reached the taxonomists! Even in a phytochemical review by Berti and Bottari (1968, p. 643), the term "wax coatings" was used, despite the more detailed chemical characterization available. This discrepancy has been mentioned several times in the literature (e.g., Smith et al., 1971).

According to strict chemical definition, waxes are esters of long-chain fatty acids with long-chain primary monovalent alcohols, in contrast to fats and oils, which are composed of glycerol esters. According to botanical terminology, waxes are less strictly defined, and include other fatty acid esters, paraffins, primary and secondary alcohols, ketones, and free n-fatty acids (Kreger, 1958). Such substances may produce bluish-white hues on the surface of some ferns, but do not form the farina of the Gold and Silver Ferns, although some paraffins may be present as occasional minor components. I recommend the use of the neutral terms "farina" and "farinose" in describing these coatings, both in ferns and in primulas, for these terms do not interfere with chemical definitions. These terms already have been used by some authors (e.g., Knobloch, 1976).

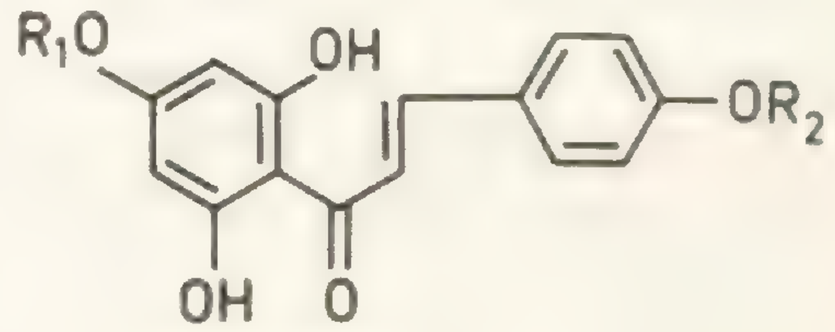
CHEMICAL INVESTIGATIONS OF FLAVONOIDS

Pityrogramma.—The first chemical analysis of the farina in *Pityrogramma* was carried out by Blasdale (1893, 1903) on *P. triangularis* (Kaulf.) Maxon. He isolated an ether-soluble, yellow substance which he called "ceroptene," and which he recognized as a benzene derivative, although he did not know its molecular structure. Using modern methods like ultraviolet, infrared, and mass spectros-

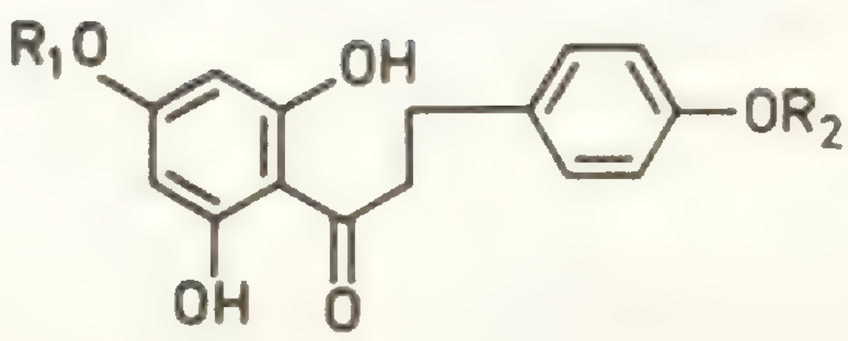
copy, Nilsson (1959) established the structural formula for ceroptin as that of a chalcone-like substance (*Fig. 3*, compound *1*).[1] Zopf (1906) isolated a red substance from *P. chrysophylla and "P sulphurea"*[2] which he called "gymnogrammene" and from *P. calomelanos* a white substance he called "calomelanene." He observed that the color of gymnogrammene depended on the shape and size of the



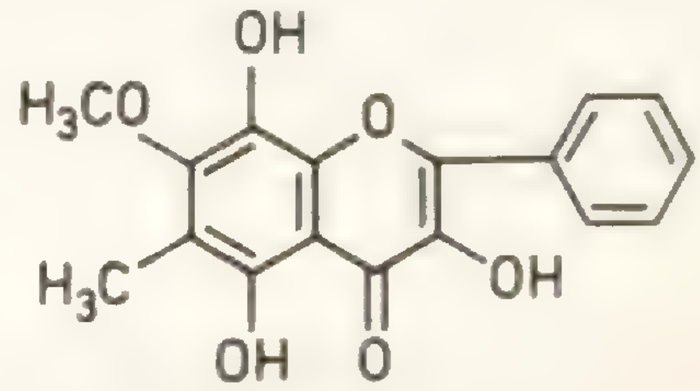
1 Ceroptin



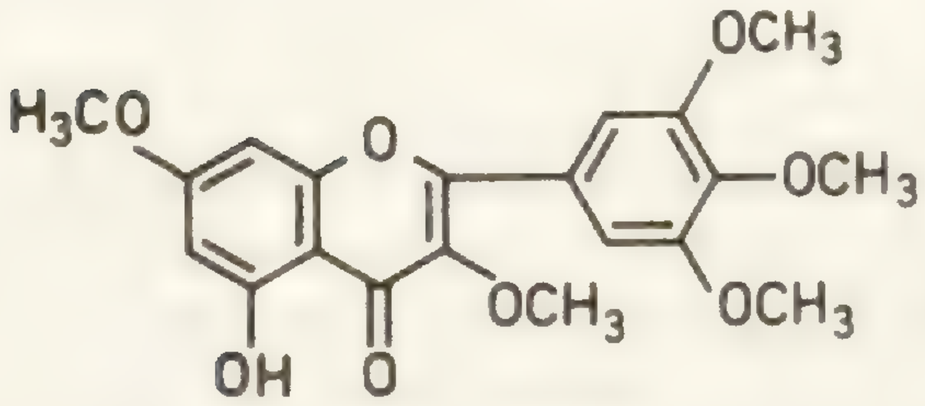
Chalcones
2 $R_1 = CH_3$, $R_2 = H$
3 $R_1 = R_2 = CH_3$



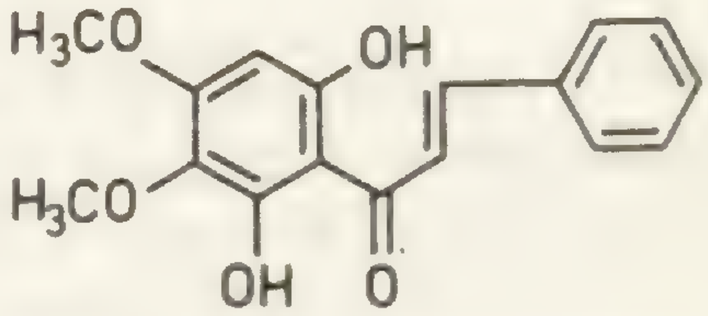
Dihydrochalcones
4 $R_1 = CH_3$, $R_2 = H$
5 $R_1 = R_2 = CH_3$



6 Pityrogrammin



7 Combretol



8 Onychium-chalcone

FIG. 3. Structures of some fern flavonoids.

crystals. Actually, the farinose coating of the fern appears yellow due to the small crystals. Gymnogrammene is orange-yellow in solution, and the dry, coarsely crystalline product can be deep red. Nilsson (1961b) obtained a similar material from the Gold Fern *P. chrysophylla* var. *heyderi* (Lauche) Domin, and he recognized that it was a mixture of two chalcones, compounds *2* and *3*. He supposed that the second chalcone was identical with gymnogrammene. However, repeating Zopf's isolation procedure, I found that gymnogrammene must have been a mixture of *2* and *3* in about equal parts (Wollenweber, 1976a). From the Silver

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[1]Here and below the compounds mentioned in the text are given numbers in italics corresponding with those used in *Figs. 3* and *4* and in *Table 1*.

[2]Presumably some other species, as *P. sulphurea* is known to have a unique flavonoid pattern unlike that of *P. chrysophylla*.

Fern *P. chrysophylla* var. *marginata* Domin, Nilsson (1961a) isolated and identified a mixture of the corresponding dihydrochalcones *4* and *5*. Compound *5* is presumably identical with Zopf's calomelanene (Wollenweber, 1976a). The yellow form of *P. calomelanos* was investigated by Bohm (1968), who by indirect evidence recognized chalcone *3* as the main component of the farina. Star and Mabry (1971) found the dihydrochalcone *5* as the major component in the white form of the same species, but dihydrochalcone *4* in *P. tartarea* (Cav.) Maxon, together with flavone *27* and flavonol *14*. In the *P. triangularis* species complex, Smith et al. (1971) found chemotypes which mainly produce ceroptin *1* and the new flavone pityrogrammin *6*, whereas others produce methyl ethers of kaempferol (*15*, *18*). It should be stressed that no other species has been found in the investigations of Star (1977) and Dietz (1978) to form ceroptin. From *P. chrysoconia* I was able to identify flavonols *9* and *11* (Wollenweber, 1972), and later I found that the light yellow farina of *P. austroamericana* is composed of chalcone *3* and dihydrochalcone *5*. The thick, white coating on the under surface of the fronds of *P. lehmannii* Hieron. from Colombia consists mainly of dihydrochalcone *5* (Wollenweber, 1976a).

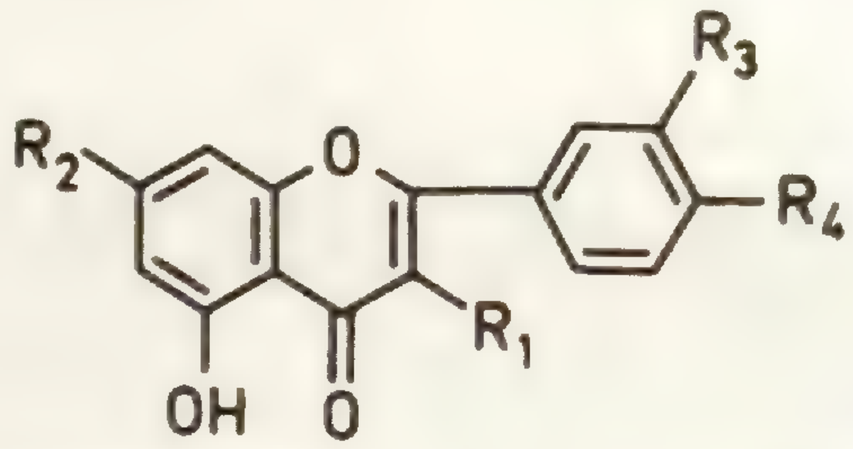

FIG. 4. General structure of flavonols and flavones. See *Table 1* for the chemical structures of groups R_1 through R_4.

Cheilanthes.—Until recently only two species of *Cheilanthes* had been investigated for farina composition. Erdtman et. al (1966), in *C. farinosa* from Taiwan, found methyl ethers of kaempferol (*18* and *19)* and one other substance which, based on the melting point and from our own observations, must be apigenin dimethyl ether *29*. In addition to these three flavonoids, Rangaswamy and Iyer (1969) found another methyl ether of kaempferol *(16)* in *C. farinosa* from South India. It is obvious that, depending on the origin of the material, additional flavonoids may occur or one or the other substances of the basic pattern may be missing. Sunder et al. (1974) identified the kaempferol derivatives *16* and *19* and apigenin methyl ether *27* in *C. longissima* (apparently an unpublished name) from the Himalayas. Recently Wollenweber (1976b) found these and other substances in *C. albomarginata* C. B. Clarke, *C. bullosa* Kunze, *C. grisea* Blanf., and *C. rufa* D. Don. *Cheilanthes kuhnii* Milde var. *brandtii* (Fr. & Sav.) Tagawa has been shown by Serizawa and Wollenweber (1977) to produce a farina very similar to that of *C. farinosa*. The sticky exudate of *C. viscida* Davenp. contains apigenin and its methyl derivatives (*26-29*), probably together with terpenoid materials. Additional species are under investigation. *Figure 4* shows the general structure of all known fern aglycones and *Table 1* enumerates them.

Notholaena.—Prior to the report of Wollenweber (1976b), no flavonoid data were published for *Notholaena*. This report contained results from individual specimens of *N. candida* (Mart. & Gal.) Hooker var. *candida, N. schaffneri* (Fourn.) Underw. var. *nealleyi* (Seaton) Weath., and *N. standleyi* Maxon. These species also produced some compounds which occur in *Cheilanthes*, and *N. candida* var. *candida* excretes a very rare pentamethyl ether of myricetin, combretol *7*. Results for many more species, mostly from several specimens each, recently were published by Wollenweber (1977a, b).

TABLE 1. FLAVONOLS AND FLAVONES FOUND AS COMPONENTS OF FERN FARINA.

Flavonols (R_1 = OH)

9 Galangin (R_2 = OH, R_3 = R_4 = H)
- *10* Galangin-3-methyl ether
- *11* Galangin-7-methyl ether

12 Kaempferol (R_2 = R_4 = OH, R_3 = H)
- *13* Kaempferol-3-methyl ether
- *14* Kaempferol-7-methyl ether
- *15* Kaempferol-4'-methyl ether
- *16* Kaempferol-3,7-methyl ether
- *17* Kaempferol-3,4'-methyl ether
- *18* Kaempferol-7,4'-methyl ether
- *19* Kaempferol-3,7,4'-methyl ether

20 Quercetin (R_2 = R_3 = R_4 = OH)
- *21* Quercetin-3-methyl ether
- *22* Quercetin-3,7-methyl ether
- *23* Quercetin-7,3'-methyl ether
- *24* Quercetin-3,7,4'-methyl ether
- *25* Quercetin-3,7,3',4'-methyl ether

Flavones (R_1 = OH)

26 Apigenin (R_2 = R_4 = OH; R_3 = H)
- *27* Apigenin-7-methyl ether
- *28* Apigenin-4'-methyl ether
- *29* Apigenin-7,4'-methyl ether

30 Luteolin (R_2 = R_3 = R_4 = OH)
- *31* Luteolin-7-methyl ether
- *32* Luteolin-3'-methyl ether

Other genera.—There are a few species of other genera which exhibit farinose excretions. One is *Onychium siliculosum*, which produces a mixture of chalcone *2* and the new chalcone *8* (Ramakrishnan et al., 1974, as *O. auratum)*. A second is *Adiantum poiretii* var. *sulphureum (A. sulphureum* Kaulf.) which, in addition to chalcone *2*, exudes dihydrochalcone *4* and traces of flavonols *9* and *11* (Wollenweber, 1976b). *Negripteris scioana* (Chiov.) Pic. Ser. and *Sinopteris albofusca* (Baker) Ching also show a farinose deposit on the lower surface of their fronds; they are under investigation now. Lellinger (1967) reported that some species of *Pterozonium* have a yellow, orange, or reddish farina. This seems to consist of chalcones, for I have identified chalcone *3* in one specimen of *P. brevifrons* (A. C. Smith) Lellinger.

It is striking that the components of fern farina are almost exclusively methyl derivatives of flavonoids, and so are rather non-polar compounds, for flavonoids usually occur as glycosides dissolved in cell sap. Excretions on the winter buds of certain trees, e.g., *Populus* (Wollenweber, 1975a) and Betulaceae (Wollenweber, 1975b), also contain methylated flavonoid aglycones. There the necessity for lipophilic properties is more evident because these excretions are often formed by remarkable amounts of lipids (volatile oils, terpenoids, phytosterols, and fats),

and the flavonoids are dissolved in this material. The farina of *Primula* also consists almost exclusively of a pure mixture of non-polar flavonoids (Wollenweber, 1974). Excretions of secondary plant products usually are lipophilic (Lüttge & Schnepf, 1976, p. 266). It may be assumed that this peculiarity correlates with the excretion mechanism, which is almost completely unknown.

Considerable amounts of material can be excreted by farinose ferns. In *P. austroamericana,* we obtained 480 mg of flavonoids from 54 g of air-dried fronds; in *P. calomelanos,* 32 g from 1 kg; in *N. candida* var. *copelandii* (C. C. Hall) Tryon, 0.78 g from 26.2 g; and in *P. lehmannii,* which produces farina abundantly, 9.1 g from 165 g. These are amounts of 0.9-5.% of the dry weight of the fronds.

CHEMICAL INVESTIGATIONS OF OTHER COMPOUNDS

In a few exceptional cases, white farina on ferns can be due to quite different lipophilic materials. In *Cheilanthes argentea* (Gmel.) Kunze, we isolated a major component that possibly is a phytosterol; the analysis has not yet been done. *Lophosoria quadripinnata* (Gmel.) C. Chr. (Cyatheaceae), which appears glaucous rather than farinose, has a weak deposit probably consisting of a mixture of triterpenes. This material also is under investigation. The n-alkanes, which lead to the glaucous appearance of such polypodiaceous ferns as *Phlebodium aureum* (L.) J. Smith, have also been found as minor components in *Pityrogramma austroamericana* and *P. lehmannii.*

Some publications have reported the occurrence of hydrocarbons, long-chain aliphatic alcohols, fatty acids, and terpenoids in ferns. Long-chain alkanes are widely distributed; among them those with odd-numbered carbon chains (C_{25}-C_{35}) predominate. Long-chain aliphatic alcohols are found in wax esters; pentacyclic triterpenes of the hopan series are abundant in the group of isoprenoids; among the phytosterols, sitosterol is dominant (Bottari et al., 1972; Seigler et al., 1975; Jamieson & Reid, 1975; Lyttle et al., 1976). Unfortunately, it is not obvious from the cited papers whether the substances are internal components of the plants or whether they are deposited externally. The same is true for the sesterpenes (Kahn et al., 1969; Iyer et al., 1972, 1973) and the ecdyson analogues (Imai et al., 1969; Faux et al., 1970). When an extract of ground material is made, it can not be seen where the extracted substances were located. Even in some clearly farinose species like *Cheilanthes farinosa* and *Onychium siliculosum,* where whole plants have been ground and extracted only people familiar with the plants realize that the flavonoids described are of external origin. When chemical work of this kind is done, more attention should be paid to the location of the chemicals being analyzed.

FLAVONOID STRUCTURES AND FARINA COLOR

Chalcones are responsible for intense yellow coloration in most cases. The decorative Gold-back Fern *P. chrysophylla,* for example, owes its bright yellow color to chalcones *2* and *3*. The less intense yellow of *P. austroamericana* is due to a mixture of chalcone *3* with dihydrochalcone *5*. The same hue in *Adiantum sulphureum* is produced by chalcone *2* and dihydrochalcone *4*. The strong colora-

tion of *Onychium siliculosum* is due to the presence of chalcones *2* and *6*. We observed that the ratio of chalcone *2* to *6* influences the deepness of the hue. Such relationships of colors with ratios of compounds is found especially with mixtures of chalcones and dihydrochalcones, but also occurs to a lesser extent in mixtures of flavones and flavonols. The intense orange of *C. mossambicensis* Schelpe and *C. welwitschii* Hooker ex Baker is accounted for by chalcone *2*, as shown by Wollenweber (1977b).

In *Cheilanthes* and *Notholaena*, white, whitish, and weakly yellow farina dominate (except for some chalcone-colored species and varieties cited below), due to the presence of flavones and flavonols. But it is more difficult to recognize relationships between composition and farina color. In species which produce derivatives of apigenin, like flavones *26-28* in *Notholaena grayi* and *26-29* in *N. greggii* (Kuhn) Maxon, the farina is white. Pure white farinas are also encountered in *N. candida* var. *candida* (caused by two methyl ethers of myricetin, *7* and an as yet unknown tetramethyl ether) and in *N. candida* var. *copelandii* (caused by galangin (*9*) and the 3-monomethyl ethers of galangin, kaempferol and quercetin (*10*, *13*, and *21*). The white form of *N. californica* D. C. Eaton produces derivatives of apigenin (*27*) and luteolin (*30* and *31*), kaempferol (*16*), and quercetin (*21*, *22*, and *24*). The light yellow farina of *N. standleyi* consists of derivatives of kaempferol only (*12-17*). *Cheilanthes farinosa* is mostly pure white or whitish, the farina being composed of methyl ethers of apigenin (*29*), kaempferol (*14*, *18*, and *19*), and sometimes quercetin (*23*) as a basic pattern. A faintly yellowish hue may depend on quantitative differences which have not yet been analyzed, but perhaps kaempferol derivative *19* prevails. The white farina of *C. albomarginata* is due to genkwanin (*27*) and to two kaempferol methyl ethers (*14* and *16*); *C. grisea*, also white, in addition produces two kaempferol derivatives (*18* and *19*).

Besides the variation in composition, the density of the deposit and the size of the particles also may play a role in color expression.

THE FUNCTION OF FARINAS

The term secretion, according to the definition of Schnepf (1969), is to be used for exudates produced by organisms or cells as a result of their interaction with the environment, or which are produced as an immediate consequence of such interaction. The term excretion, on the other hand, refers to waste matter, the production of which is not directly related to the environment. Schnepf emphasized that a sharp demarcation of both terms is neither possible nor necessary. Thus the word excretion may well be used when talking about exudates of farinose ferns, although the term secretory glands may also be used as a general term.

Many years ago, Blasdale (1893) considered the possible function of glandular cells on *Pityrogramma* fronds and *Primula* leaves, and he remarked that their existence gave rise to speculation. In his opinion, one could not help recognizing glandular cells as a mechanism for some definite purpose, as he could not regard the material excreted as mere waste products. He found one plausible function: protection of young spores as well as the lower epidermis against "excessive

moisture," since the position and chemical nature of the farinose material keep water off the lower surface of the fronds. He thought a second role was to protect these natives of arid regions against excessive transpiration, since many allied species without glands had a thick growth of hairs or scales. Höhlke (1902) attributed to the "resin" of *Gymnogramma* (i.e., *Pityrogramma*) the function of an insect deterrent "because the plants in the greenhouse are free of destructive insects even in summer." He felt confirmed in his opinion by the observation that the coating was thick on young fronds and diminished or even vanished on old fronds, which no longer needed this protection. This misinterpretation was probably based on incomplete observation; secretory glands stand much further from each other on adult fronds than on juvenile ones because new glands do not develop during the later stages of frond growth and the glands no longer are active. Hence, the excretion material is dispersed. Partly it crumbles as a dry mass, and partly it is rinsed off by rain. Nayar (1964) states, "On mature stipes the glandular hairs shrivel, leaving powdery covering which is often lost on old stipes."

Haberlandt (1918, p. 478) stated that the physiological and ecological importance of the epidermal glands in general depends on the nature of the exudate. Apart from the possibility that in some cases useless end products of metabolism may be secreted, secretions usually have some significance, like protection against strong transpiration or against animal attack. These are the same possible functions that Blasdale and Höhlke attributed to fern glands. Bower (1923, p. 198) was convinced of the role of fern excretions as water repellents. Linsbauer (1930, p. 123) accepted primarily their role in preventing excessive transpiration. However, he regarded speculations on the ecological significance as idle. Nilsson (1959) found it tempting to speculate on the possible physiological significance of the ceroptin coating of *Pityrogramma triangularis*, and he mentioned that the β-triketones (in which he then included ceroptin) are known to exhibit antibacterial and sometimes insecticidal activity. I think some antibacterial effect can certainly be attributed to most phenolics, and this could apply to fern farina in general, but we have no proof as yet. Swain (1973) speculated about quite a different function. He assumed that the chalcones "in the sori" of *P. chrysophylla* might control some light-catalyzed reaction. However, this is quite unlikely since the chalcones are produced by glands of the epidermis. All considerations on the possible functions of fern farina may be summarized by the comment of Harborne et al. (1975, p. x) on flavones and flavonols: "The raison-d'être . . . still remains as mystery."

DISTRIBUTION OF FLAVONOIDS IN THE GENERA

All the ferns so far found to excrete flavonoid aglycones belong to the Polypodiaceae subfam. Gymnogrammoideae, and to sects. Cryptogrammeae (*Onychium*), Gymnogrammeae (*Pityrogramma* and *Pterozonium*), Adianteae (*Adiantum*), and Cheilantheae (*Cheilanthes, Negripteris, Notholaena,* and *Sinopteris*), according to the system in Engler's "Syllabus" (Melchior & Werdermann, 1954). Hooker and Baker (1868, p. 384) proposed *Gymnogramma* sect.

Ceropteris (Link) Hooker & Baker for farinose species of *Pityrogramma* and *Notholaena* sect. *Cincinalis* (Desv.) Hooker & Baker (1868, p. 373) for farinose species of *Notholaena*. Farinose *Cheilanthes* species are called *Aleuritopteris* by some authors, or are at least separated as *Cheilanthes* sect. *Aleuritpteris* (Fée) Hooker & Baker, as in Nayar (1962).

The various species of *Pityrogramma* in general produce chalcones and/or dihydrochalcones (*2-5, 8*); flavones and flavonols can occur as minor components. *Cheilanthes* and *Notholaena,* on the other hand, produce flavones and flavonols (*7* and *10-32*). Known exceptions in *Pityrogramma* are *P. triangularis* (Star et al. 1975b) and *P. chrysoconia* (Wollenweber, 1977a). In both cases, only some forms or chemotypes differ from the chalcone-dihydrochalcone scheme. Exceptions in *Cheilanthes* are *C. aurea* Baker, *C. aurantiaca* (Cav.) Moore, *C. chryosophylla* Hooker, *C. mossambicensis,* and *C. welwitschii.* These species excrete chalcones. There is also one form of *C. welwitschii* which produces a dihydrochalcone. In *Notholaena,* I know three species which exude chalcones: *N. aurantiaca* D. C. Eaton, *N. nivea* var. *flava* Hooker, and the yellow form of *N. sulphurea* (Cav.) J. Smith. Dihydrochalcones also may occur, as in *N. lemmonii* D. C. Eaton and the white form of *N. sulphurea*. Thus Bohm's (1975) statement that "*Pityrogramma* is the only fern genus known to accumulate chalcones and dihydrochalcones" is no longer true.

CHEMOTAXONOMIC EVALUATION

Alt and Grant (1960) showed that the varieties of *Pityrogramma triangularis* constitute a polyploid complex which includes diploids, triploids, and tetraploids. Smith et al. (1971) showed that correlations for these taxa exist between spore morphology, cytology, and pigment chemistry. According to the composition of farina, they distinguished four chemotypes: ceroptin type, kaempferol-methyl ether types A and B, and a type with kaempferol derivatives and ceroptin. According to their data, different ploidy levels can not be distinguished by farina analysis. The complexity of chemical and cytological variation allowed two alternative interpretations: either *P. triangularis* is one species existing as an autoploid complex and consisting of genetic variants with the same basic genome, or it is a segmental allopolyploid group with several genomes (cf. Mabry, 1973). Later, more detailed chemical investigations included the analysis of internal flavonoid glycosides (Star et al., 1975a). Diploids and tetraploids can be distinguished by this method within the ceroptin type as well as within one kaempferol methyl ether type. Thus, in *P. triangularis* var. *triangularis* four taxa can be outlined by means of chemical data. The tetraploid kaempferol methyl ether chemotype has a glycoside pattern composed of those of two diploids, and so may be of alloploid origin. The tetraploid ceroptin chemotype, on the other hand, may be of autoploid origin. Finally, n-alkanes occuring in these excretions have been investigated by Seigler et al. (1975). As expected, this class of compounds is not helpful for chemotaxonomic investigation. However, the average percentage of C_{33} lends support to the previous suggestions concerning the origin of tetraploids.

My own investigations as yet have been less far-reaching. Difficulties in obtaining plant materials and the small size of most samples received from herbaria has limited analysis to external flavonoid aglycones. Furthermore, the number of samples received of individual species is still very small. Nevertheless, from the high number of species analyzed, certain trends can be observed.

As stated above, excretions of chalcones and dihydrochalcones dominates in *Pityrogramma*. Apart from the exceptions cited, the occurrence of these substances at present appears to be a genus-specific character. When so far unidentified minor components are included, this suggestion is strongly supported. Thus, an Indian *P. calomelanos* can not be distinguished from a South American *P. dealbata*. On the other hand, in some species, small differences in external flavonoid patterns are noted, the meaning of which is under investigation. The differences probably are not sufficient to consider the plants as different chemotypes. The presumed specificity of farina composition in a few species (Dietz, 1978) still has to be verified.

As far as *Cheilanthes* and *Notholaena* are concerned, it is disappointing that no sharp delimitation of these genera, which are controversial in the taxonomic literature (cf. Knobloch, 1976), is possible by farina analysis. In both genera, methyl ethers of kaempferol, quercetin, and apigenin are synthesized above all others (see *Fig. 4* and *Table 1*). Nevertheless, there are some interesting peculiarities within the genera, even though only a few specimens per species have been analyzed as yet. *Notholaena bryopoda* Maxon (compounds *13, 16, 19*), *N. grayi (26-28)*, and *N. greggii (26-29)* have species-specific flavonoid patterns. Other species show unique patterns, too, but their substances have not yet been identified. *Cheilanthes* also has species/specific flavonoid patterns (Wollenweber, 1976c). The basic patterns may vary slightly by the addition of inconstant compounds. In this infraspecific variation I am inclined to see an expression of variability in biosynthetic capacity, just as we are used to seeing variability in morphological characteristics. Certainly interpretation becomes more difficult when more complicated flavonoid patterns in species like *N. incana* Presl or *N. standleyi* are considered. Infraspecific as well as infra- and inter-populational variation can not be studied from single specimens; extensive field collecting is necessary to accomplish this.

In some cases, variety-specific flavonoid patterns may occur. For example, five specimens of *N. candida* var. *copelandii* are characterized by the 3-methyl ethers of galangin, kaempferol, and quercetin, *10, 13, 21*. Unfortunately, the poly-0-methyl ethers of myricetin (*7* and unknown) are not so constantly encountered in all five specimens of var. *candida*. Nevertheless, evaluated jointly with the additional unknown components, they are typical for this variety and permit inclusion here of three specimens which I received unnamed to variety. Similar examples are known in other *Notholaena* and *Cheilanthes* species.

Chemotypes may exist, e.g., in *N. affinis* (Mett.) Moore and in *N. californica*, where classic taxonomy does not distinguish varieties. Tryon (1965, pp. 47-48) describes the lower lamina surface of *N. affinis* as having "pale yellow to yellow

(rarely white) indument." At present I have six samples of this species, all with light yellow farina. Four show kaempferol (*12*) as the predominant or even sole component; apigenin (*26*) and isokaempferid (*13*) can occur as minor components. Two collections from Costa Rica, however, show unknown compounds instead; the major component of the farina was identified as a flavonol with butyryl side chain (Wollenweber et al., 1978). It is possible to presume the existence of chemotypes, but as yet it is not known whether these are correlated with populations. For *N. californica,* Tryon (1956, p. 74) wrote, ". . . lower [surface] whitish to usually yellow ceraceous." The yellow farina consists of a series of unknown substances now under investigation which show an identical pattern in the eight samples available. But the white farina of three other samples consists of distinct and constant methyl ethers of flavonoids. Here, too, one can presume the existence of chemotypes. It must be left to the taxonomists whether it is justifiable to establish varieties or not. But in both cases both color differences and differences in flavonoid pattern exist.

Tryon (1962, 1964) did not take into account "wax color forms" in ferns in which the color is not correlated with any other characteristic or with geography. For *P. chrysoconia,* he wrote, "Plants with white wax on the leaves and those with yellow wax both occur nearly throughout the range of species and there seems to be no reason to recognize these variants." For *P. chrysophylla,* he wrote, "The white and yellow color forms, although especially striking in this species, do not merit recognition." For *P. calomelanos* and *P. tartarea,* however, he wrote, "In these species the strong correlation of the character with geography seems to provide it with an importance it would otherwise not have." Tyron distinguishes varieties of these species by the farina color (*P. calomelanos* var. *calomelanos,* var. *aureoflava* (Hooker) Weath. ex Bailey, and var. *ochracea* (Presl) Tryon; *P. tartarea* var. *tartarea,* var. *aurata* (Moore) Tryon, and var. *jamesonii* (Baker) Tryon).

Species with very variable patterns of external flavonoids, like *N. schaffneri* in which each sample is different from every other one and no correlation with the established varieties *schaffneri* and *nealleyi* can be detected, are still very puzzling and dictate caution in interpreting flavonoid data In addition, special difficulties are expected with those species in which different colors are observed on a single plant, possibly depending on the age of the frond or plant (Tryon, 1956). These phenomena require further investigation, as do flavonoid studies in general. I would appreciate contributions of fresh material and herbarium specimen fragments (even of widespread species) to support such studies.

My investigations reported here were initiated by Prof. W. Hagemann, of the University of Heidelberg, who first supplied samples of farinose ferns. In view of the rarity of many species and their restriction to tropical regions of the world, the work on this subject would have been impossible without the kind support of many pteridologists. To all of them I am greatly obliged, and I wish to express my gratitude. Thanks are also due to Prof. W. Ullrich, of the Technische Hochschule Darmstadt, for critically revising the manuscript and for his kind help with the English translation.

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SHORTER NOTES

THE SELAGINELLA APODA COMPLEX IN IOWA.—In 1958 R. F. Thorne and R. L. Hulbary discovered the only Iowa locality for specimens of the *S. apoda* (L.) Spring complex (Muscatine Co., *Thorne 20171*, UI). This population also represents the most northwesterly station of the *S. apoda* complex in North America. The population occurred in a seepage bog at the base of a sandy bluff. Shortly after the discovery of this *Selaginella*, the locality was ditched, drained, and placed into intensive agricultural use. The population was presumed to have been exterminated. In 1975, one of us (JHP) visited the locality and discovered that the population was still extant. Drainage and grazing had great impact on the larger vascular plants, but the prostrate *Selaginella* appeared to have been promoted by the disturbance. The population now exists as a dense ground cover and forms a strip 1–2 m wide and over 200 m long. In addition, the population, which was not fertile in 1958, was abundantly fertile in 1975–1977.

The plants originally were identified as *S. apoda* and have subsquently been so treated by Iowa workers (e.g., Peck., J.H., 1976. The pteridophyte flora of Iowa. Proc. Iowa Acad. Sci. **83:** 143–160). Recently, however, investigations by one of us (WRB) led to the description of *Selanginella eclipes* Buck as a species distinct from *S. apoda* (Buck, W. R., 1977. A new species of *Selaginella* in the *S. apoda* complex. Canad. J. Bot. **55:** 366–371). *Selaginella eclipes* is distinguished from *S. apoda* by features of the megaspore wall and by leaf morphology. *Selaginella eclipes* is found to the north and west of *S. apoda*, and occurs in an arc from Oklahoma northeast to the Great Lakes region and then northeastward along the St. Lawrence River. The Iowa population of the *S. apoda* complex was not examined during the original study of *S. eclipes*. Subsequently, Iowa specimens were examined and found to be *S. eclipes*. *Selaginella apoda* (L.) Spring is therefore excluded from the Iowa pteridophyte flora. The purpose of this note is to call attention to the importance, persistence, and identity of the Iowa population.—*James H. Peck, Dept. of Biology, University of Wisconsin-La Crosse, La Crosse WI 54601* and *William R. Buck, Dept. of Botany and Herbarium, University of Michigan, Ann Arbor, MI 48109.*

POLYSTICHUM LONCHITIS FOUND IN THE BLACK HILLS.—A single plant of *Polystichum lonchitis* (L.) Roth was found in the Black Hills of Wyoming on September 4, 1977. The location is in Crook County, in Upper Dugout Gulch about 8 miles south of Beulah and about 1.5 miles west of the South Dakota border, at an elevation of 4800 feet. The plant was growing in a damp ravine under Paper Birch, *Betula papyrifera* Marsh., and Beaked Hazelnut, *Corylus cornuta* Marsh. The plant was vigorous and had numerous fronds, several of which were removed to be deposited at Harvard University (GH) and the University of Wyoming (RM) (*Dorn 3042*). The closest known localities are about 265 miles

southwest, in Carbon County, Wyoming. The species also occurs in northwest Wyoming, south-central Montana, and further west. This new locality is not unexpected since the species distribution now parallels that of several other vascular plants which jump from the Rocky Mountains, to the Black Hills, to the upper Great Lakes, and to the Gaspé area of Québec.—*Robert D. Dorn, Box 1471, Cheyenne, WY 82001.*

ON THE DISTRIBUTION OF LYCOPODIUM FLABELLIFORME IN ILLINOIS.—The Ground-pine, *Lycopodium flabelliforme* (Fern.) Blanch., was collected on 11 Oct 1976 from the northwest part of Lake Argyle State Park, McDonough County, Illinois (NE 1/4 of S36, T6N, R4W). This collection is the first report of this species in western Illinois and the fourth report of a native station for the state. It is interesting to note that the three previously reported native stations, in Pope, Ogle and Crawford Counties,[1] are on the southern, northern, and eastern perimeters of the state, and McDonough County is at the western edge. *Lycopodium flabelliforme*, therefore, may occur in interior Illinois counties as well. Three adventive stations in two other peripheral northeastern counties (Ogle and Cook) have also been reported.[2] The McDonough County population of *L. flabelliforme* is about 112 miles from the nearest of the two reported Iowa collections and 140 miles from the nearest Illinois location; the species has not been reported from Missouri.[3]

The McDonough County plants were scattered in a shaded area of about 30 ft^2 on a slope several feet above the lake margin. Cones were not present. The canopy trees of the collection site were *Acer saccharum* Marsh., with *Ostrya virginiana* (Mill.) K. Koch and *Ulmus rubra* Muhl. the dominant understory trees. The mesic deciduous woodland is a relatively young, secondary one. Characteristic herbaceous vascular plants included *Cystopteris fragilis* (L.) Bernh., *Adiantum pedatum* L., *Equisetum arvense* L., *Sanguinaria canadensis* L., *Hepatica acutiloba* DC., and *Dicentra cucullaria* (L.) Bernh. Mosses present were *Mnium cuspidatum* Hedw., *Brachythecium acuminatum* (Hedw.) C. F. Austin, and *Brylnia graminicolor* (Brid.) Grout. The soil was a sandy loam over sandstone and had a pH of 6.2

A voucher specimen (*R. D. Henry 4052*) has been deposited in the Western Illinois University Herbarium (MWI) at Macomb.—*R. D. Henry* and *A. R. Scott, Department of Biological Sciences, Western Illinois University, Macomb, IL 61455.*

---

[1] Phillippe, L. R. 1971. A new distribution record for Lycopodium flabelliforme in Illinois. Trans. Ill. State Acad. Sci. **64**(4): 399.

[2] Mohlenbrock, R. H. 1967. The Illustrated Flora of Illinois: Ferns. Southern Illinois University Press, Carbondale, p. 31.

[3] Wilce, J. H. 1965. Section Complanata of the genus Lycopodium. Nova Hedw. **19:** 142,197,200.

REVIEW

"A MONOGRAPH OF THE FERN GENUS BOLBITIS (LOMARIOPSIDACEAE)", by E. Hennipman, Leiden Botanical Series 2: xii + 331 pp., 12 pl., 87 fig. 1977. Leiden University Press. ISBN 90-6021-405-6. $38.50/Dfl. 92.—This is an impressive and intricate work, unquestionably the most complete monograph that exists for any pantropical fern genus. Hennipman recognizes 44 species (a reduction from the 97 of Copeland) and 13 hybrids. He divides *Bolbitis* into ten series, based primarily on venation, spore morphology, rhizome anatomy, and rhizome scales. One of these series *(Egenolfianae)* comprises the species often included in the segregate genus *Egenolfia,* but Hennipman offers convincing reasons for treating it as a part of *Bolbitis*. Further, he suggests that the free-veined series *Egenolfianae* may represent a derived condition in a genus that is usually characterized by anastomosing and reticulate venation. Generally, the series seem well characterized; however, no key is provided and only 34 of 44 species are placed in this scheme, so that it is a little difficult to understand series limits. Hennipman postulates that several of the ten unplaced species may have arisen through hybridization between species of different series. One American species *(B. bernoullii)* is postulated to have arisen through hybridization between *B. lindigii* and a species of another genus, possibly *Polybotrya,* a suggestion that cries out for experimental verification. If Hennipman is right, hybridization has been extremely important in the evolution of *Bolbitis* and, by extrapolation, in tropical ferns in general.

The taxonomic account includes keys (separate keys for American, African, and Asian–Pacific *Bolbitis*), descriptions, synonymy, distribution maps, and excellent illustrations. There is a thorough introductory account of such topics as morphology and anatomy, karyology, habitat, juvenile leaf characters, intra- and inter-generic relationships, and biogeography. One of the most difficult aspects in dealing with *Bolbitis* is the great variation in leaf morphology within species, many of which show a succession of leaf forms (heteroblastic series). Certain precociously fertile juvenile forms had previously been treated as distinct species, but Hennipman, through the study of herbarium specimens and living plants, has convincingly shown their identity with more developed forms.

Several unusual or novel features of the taxonomic treatment are exemplary. There is an abbreviated list of specimen citations: where species are common Hennipman gives the number of collections seen in a given political unit; where uncommon or rare, collector, number, and herbarium acronym are cited. To compliment this list, there is a complete index of collections organized alphabetically by collector. Following the description of each species, there are extensive notes on habitat, elevation, relationships, variability, aberrant specimens, typification, and spore morphology. The last-named character is given more complete coverage than in any fern monograph I have seen, tropical or temperate.

One possible source of confusion is the treatment of certain "taxa" as hybrids and others as species of hybrid origin. Hennipman attributes abnormal spores or aborted spore mother cells to most of the hybrids. However, *Bolbitis* × *lancea, B.*

× *prolifera*, and *B.* × *sinuosa* nm. *foxii* are all described as having "normally shaped spores." It is also a little disconcerting, even frightening, that most of the 44 species described by Hennipman have some specimens (even a majority, e.g., in *B. pergamentacea)* that show abnormal spores. Curiously, there are many more inter-series hybrids (13) than intra-series hybrids (3).

If the quality of this monograph is to be approached for other fern genera, there is plenty for all pteridologists to do for the foreseeable future.—*Alan R. Smith, University Herbarium, Department of Botany, University of California, Berkeley, CA 94720.*

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The Taxonomic Status of Selanginella eatonii

WILLIAM R. BUCK*

Selaginella eatonii Hieron. ex Small has long been relegated to synonymy under *S. armata* Baker, but actually it is a distinct species. The plants are among the smallest known in this predominantly tropical genus. *Selaginella eatonii* and the West Indian *S. armata* are both members of subg. *Stachygynandrum* (Pal. Beauv.) Baker, which is characterized by having dorsiventrally flattened shoots comprising two lateral rows of larger leaves plus two medial rows of smaller leaves. According to Baker's (1883-1885) scheme of classification, *S. eatonii* is closely related to the other heterophyllous *Selaginellae* of eastern North America, namely *S. apoda* (L.) Spring, *S. eclipes* Buck, and *S. ludoviciana* A. Braun.

When J. K. Small (1918, p. 67) originally described *S. eatonii*, he credited Hieronymus with being the author. No specimens of it were cited, although Small reported the plant as growing on limestone in the "Everglade Keys;" he also stated that the plant was first collected in 1903. The species is quite rare in South Florida.

Much of the pertinent literature has either been misleading or in error. Small (1938, p. 422) transferred *S. eatonii* to the genus *Diplostachyum*, which was erected by Palisot de Beauvois to accommodate many of the heterophyllous species of *Selaginella*. Today this segregate genus is mostly unaccepted. Prior to this time, Britton and Millspaugh (1920, p. 477) reported *S. eatonii* as occurring in the Bahamas. However, Alston (1952, p. 44), a world authority on *Selaginella*, cited their Bahamian material as *S. bracei* Schmidt, which also is a plant of diminutive habit; it was described from Andros and Abaco Islands, Bahamas. Alston (1952, p. 43; 1955, p. 246) placed *S. eatonii* in synonymy under *S. armata*, which was described from Cuba. Unfortunately, *S. eatonii* was not typified by Alston in his publications, nor were descriptions given to any of the species; only keys, specimen citations, and brief annotations were provided. Subsequent authors who have dealt with the South Florida species, e.g., Wherry (1964, p. 276), Ward (1968), Long and Lakela (1971, p. 69), Mickel (1974), and Lakela and Long (1976, p. 27), have used the name *S. armata*.

Recent examination of type material of the three species in question has led to the conclusion that Alston (1952, 1955) was mistaken in equating *S. eatonii* and *S. armata*. Rather, *Selaginella eatonii* is synonymous with *S. bracei*. However, as *S. eatonii* was described in 1918 and *S. bracei* in 1924, *Selaginella eatonii* has to be the correct name for the species. The following key, along with descriptions and illustrations of the type material of the three species, as well as my lectotypification of *S. eatonii* and *S. bracei*, should prevent further misunderstanding, especially of South Florida material.

---

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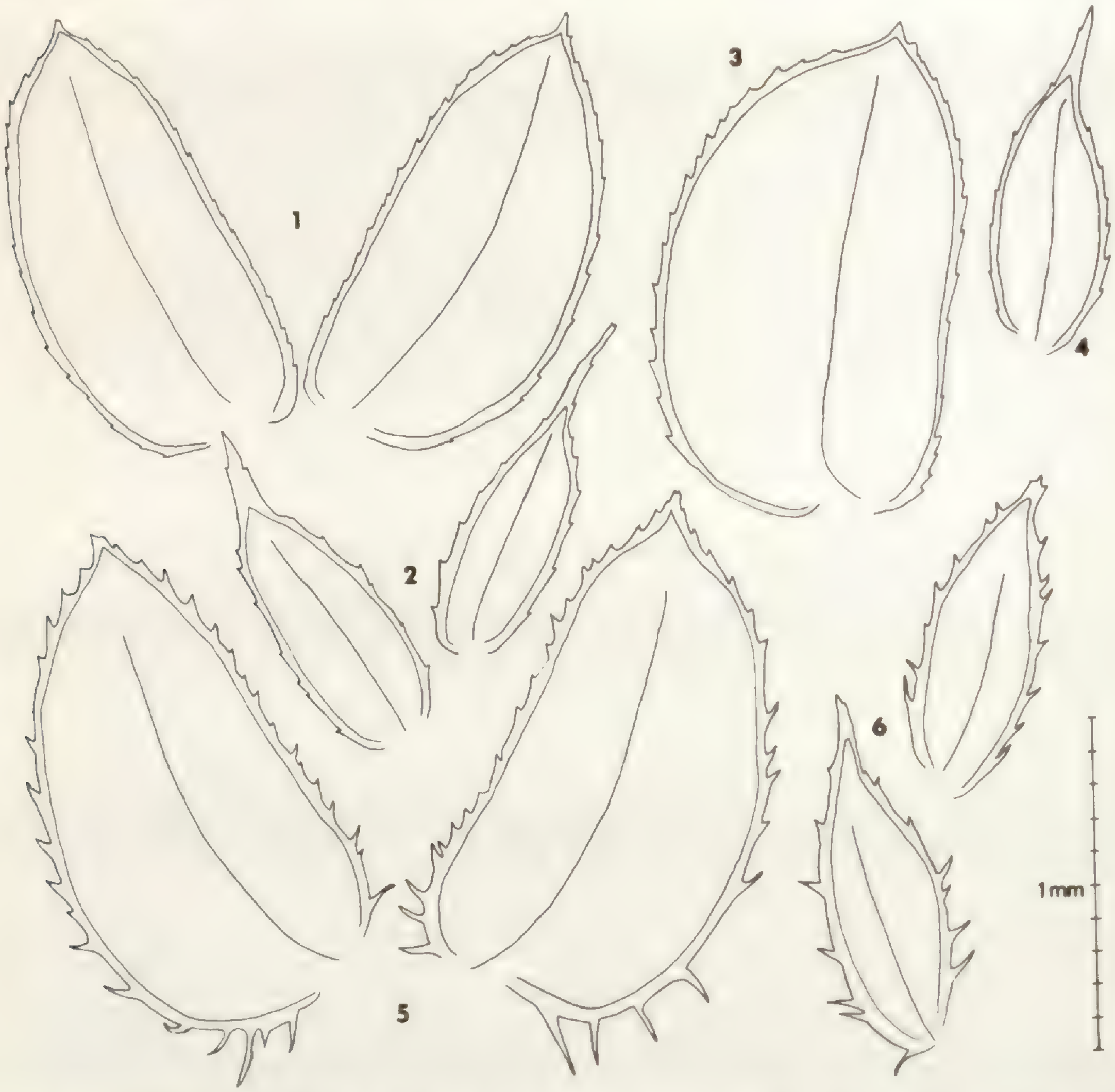
Leaf margins serrate, light-green; stomata on abaxial side of lateral leaves and adaxial side of medial leaves scattered over the whole laminar surface; megaspores yellow to orange, less than 220 μm in diameter..... 1. *S. eatonii*

Leaf margins ciliate, especially at the base, hyaline; stomata on abaxial side of lateral leaves and adaxial side of medial leaves arranged linearly only along the midrib; megaspores white, more than 220 μm in diameter..... 2. *S. armata*



FIGS. 1-6. Leaves of *Selaginella*. FIGS. 1-2. *S. eatonii* (*Eaton* in 1903, NY). FIG. 1. Lateral leaves. FIG. 2. Medial leaves. FIGS. 3-4. *S. bracei* (*Brace 1834*, NY). FIG. 3. Lateral leaf. FIG. 4. Medial leaf. FIGS. 5-6. *S. armata* (*Wright 3908*, NY). FIG. 5. Lateral leaves. FIG. 6. Medial leaves.

1. **Selaginella eatonii Hieron. ex Small, Ferns Trop. Florida 67, fig. 1918. Figs. 1–4.**

Selaginella bracei Hieron. ex O. C. Schmidt, Repert. Sp. Nov. Fedde **20:** 156. 1924, *syn. nov.* LECTOTYPE: Marsh Harbour, Great Abaco Island, Bahamas, 21 Dec 1904, *L. J. K. Brace 1834* (NY). SYNTYPES: Marsh Harbour, Great Abaco Island, Bahamas, *Brace 1618* (NY); Mastic Point, Andros Island, *Brace 7024, 7113* (both NY).

Diplostachyum eatonii (Hieron. ex Small) Small, Ferns Southeast. States 422. 1938.

LECTOTYPE: About lime-sinks, border of Everglades, Black Point Creek, Dade County, Florida, 13 Nov 1903, *A. A. Eaton 265* (NY; isolectotype US not seen).

Plants yellow-green, small, creeping over limestone with mosses; stems 1-4 cm long. Lateral leaves ovate, gradually acute, 1.25-1.4 mm long, 0.75-0.9 mm wide, serrate; midrib ending 75-125 μm below leaf apex; margin light-green, composed of 2-4 rows of linear, slightly to distinctly papillose cells, papillae arranged longitudinally; upper epidermal cells ± isodiametric, many-sided, with several small chloroplasts per cell, lower epidermal cells ± rectangular, 2-6 times longer than wide, with strongly sinuous walls; stomata of abaxial (aligular) surface scattered over whole lamina, those of the adaxial (ligular) surface confined to the margin. Medial leaves lanceolate, long-acuminate, 1.0-1.2 mm long, 0.3-0.35 mm wide, serrate; midrib ending 300-350 μm below leaf apex; margin light-green, composed of 1-3 rows of linear, slightly to distinctly papillose cells, the papillae arranged longitudinally; apex long-acuminate, serrate, composed of linear cells continuous from the leaf margin, not papillose; epidermis as in lateral leaves; stomata on adaxial (ligular) surface only, scattered over the whole lamina. Strobili 2-5 mm long; sporophylls ovate, ca. 1.4 mm long, 0.75 mm wide, acuminate, serrate; margin as in the trophophylls; midrib ending ca. 400 μm below the leaf apex, strongly ridged on the abaxial side from linear, papillose cells, spinose, the spines ending at about the costal apex; stomata on the abaxial surface only, scattered over the whole lamina. Megaspores yellow to orange, ca. 200 μm diameter, slightly roughened to almost smooth. Microspores orange, ca. 30 μm in diameter, rough.

2. **Selaginella armata Baker, J. Bot. Brit. & For. 22: 90. 1884.** **Figs. 5–6.**

Type: Cuba, *C. Wright 3908* (K *fide* Alston, 1952; isotypes BM, NY!).

Plants green, small, creeping; stems 1-4 cm long. Lateral leaves oblong-ovate, abruptly tapering, ca. 1.5 mm long, 0.8-0.9 mm long, ciliate, especially near the base; midrib ending 250-400 μm from the apex; margin hyaline, composed of 2-5 rows of linear cells, smooth to slightly papillose, cilia single-celled, becoming longer toward the base, to 150 μm long; upper epidermal cells ± isodiametric, almost circular, with a single large chloroplast per cell, lower epidermal cells ± rectangular, 4-6 times longer than wide, with strongly sinuose walls; stomata of abaxial surface confined to the midrib region, those of the adaxial surface confined to the margin. Medial leaves elliptic-lanceolate, short-acuminate, 1.0-1.2 mm long, 0.3-0.35 mm wide, ciliate; midrib ending 300-400 μm below the apex; margin hyaline, composed of 2-4 rows of linear, smooth to slightly papillose cells, the cilia single-celled, becoming longer toward the leaf base, to 130 μm long; apex short-acuminate, with only a single pair of linear cells confluent at the apex; epidermis as in the lateral leaves; stomata on the adaxial surface only, arranged longitudinally along and over the midrib. Strobili 2-5 mm long; sporophylls ovate, ca. 1.75 mm long, 0.75 mm wide, short-acuminate, ciliate; margin as in the trophophylls but more distinctly papillose; midrib ending ca. 500 μm below the leaf apex, spinose but not ridged at the back, the spines ending above the costal apex. Megaspores white, ca. 230 μm in diameter, reticulate. Microspores orange, ca. 30 μm in diameter, ± granular.

Selaginella eatonii is the correct name for the native heterophyllous *Selaginella* of South Florida, and *S. armata* is excluded from the North American flora. The two species are most easily separated on the basis of the serrate versus ciliate leaves in *S. eatonii* and *S. armata*, respectively. However, numerous additional diagnostic characters are present at the microscopic level. Most conspicuous of these are the differences in stomatal distribution. In *S. eatonii* the stomata of the aligular surface of the lateral leaves and of the ligular surface of the medial leaves are scattered over the whole laminar surface, whereas for the same laminar re-

gions in *S. armata*, the stomata are confined to the midrib area. Stomatal distribution was first suggested by McNab (1887) as of possible taxonomic importance in the genus. More recently, Buck and Lucansky (1976) used it as an aid in the separation of *S. apoda* and *S. ludoviciana*. An additional microscopic character useful in separating *S. eatonii* from *S. armata* is the distance from the distal end of the costa to the apex of the lateral leaf. In *S. armata* the midrib ends 250-400 μm from the apex, whereas in *S. eatonii* the equivalent distance is only 75-125 μm. Megaspore differences also exist between the two species. Although Hellwig (1969) found megaspore color of little use in segregating higher taxonomic groups of *Selaginella*, it is of value in separating these species. In *S. eatonii* the megaspores are yellow to orange; those of *S. armata* are white. Also the megaspores of *S. armata* are larger than those of *S. eatonii*. Further research on the apparent plastid differences between *S. eatonii* and *S. armata* would be rewarding.

Dr. C. E. Delchamps, of the University of Miami, Coral Gables, Florida, planned to contribute ecological data from personal field experience with *S. eatonii*. Unfortunately Dr. Delchamps died prior to contributing. I am indebted to him for first calling this problem to my attention by sending me living South Florida material.

I thank Dr. John Mickel of the New York Botanical Garden for permission to examine the type material and for the use of facilities while I was visiting there. I am also grateful to Drs. Howard Crum and W. H. Wagner, Jr. for comments and criticisms concerning the manuscript.

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Microreplicas as a Technique for Rapid Evaluation of Surface Silica Micromorphology in Equisetum

RICHARD L. HAUKE*

The genus *Equisetum* has caused problems to field botanists and herbarium workers because the species are often difficult to identify. The general morphology is so plastic and responsive to environmental influence that the same species can look quite different under different circumstances, and two different species can under certain conditions closely resemble one another. One source of characters which has recently come to the foreground is the micromorphology of surface silica.

Equisetum has long been noted for its ability to take up silicon dioxide and deposit it on the surface of the plant as a hard, outer coat. For this reason, certain species have been used to scour pots and pans (scouring rush), or to polish wood (joiner's rush). The silica deposits have been suspected of varying among species, and in studying subgenus *Hippochaete*, I used the silica profile of the branch ridges as a character in distinguishing *E. giganteum*, *E. myriochaetum*, and their hybrid, *E.* × *schaffneri* (Hauke, 1963). I also illustrated the silica rosettes in the valleys of *E. ramosissimum* subsp. *debile*. Milde (1867) had illustrated these, as well as some vague differences of surface pattern among species of subg. *Equisetum*, particularly on the stomata.

With development of the Scanning Electron Microscope (SEM), surface features of biological entities have become more amenable to study. Various people have used this technique to look at *Equisetum* (Laroche, 1968, 1969a, 1969b; Laroche et al, 1970; Kaufman et al., 1971; Page, 1972, 1974; Tanowitz, 1975; Dayanandan, 1977; Lawry, unpublished). Page (1972) revised the taxonomy of *Equisetum* subg. *Equisetum* largely utilizing silica micromorphology. Since the SEM technique is somewhat laborious and requires special equipment, it does not lend itself to convenient and rapid evaluation of surface micromorphology of a number of specimens from different localities, of plants of different ages, or of different parts of the same plant. Apparently Page looked at only one specimen for each species, and did not appreciate the possibility of silica pattern variation within a plant or between plants of the same species.

The silica micromorphology does show some consistent characters by which species of *Equisetum* subg. *Equisetum* can be recognized (Hauke, 1978), and it is useful in helping to identify aberrant specimens. However, it is impractical for the working taxonomist, who must sort stacks of specimens, to stop and prepare for the SEM material from a problematic specimen, assuming he even has ready access to a scanning electron microscope.

I sought a practical alternative to the SEM for rapidly evaluating surface silica micromorphology of herbarium specimens of *Equisetum*. The technique I adopted is the "microreplica" method, as published in the Turtox News some years ago. I have used this successfully on dried, pressed herbarium specimens. It works best

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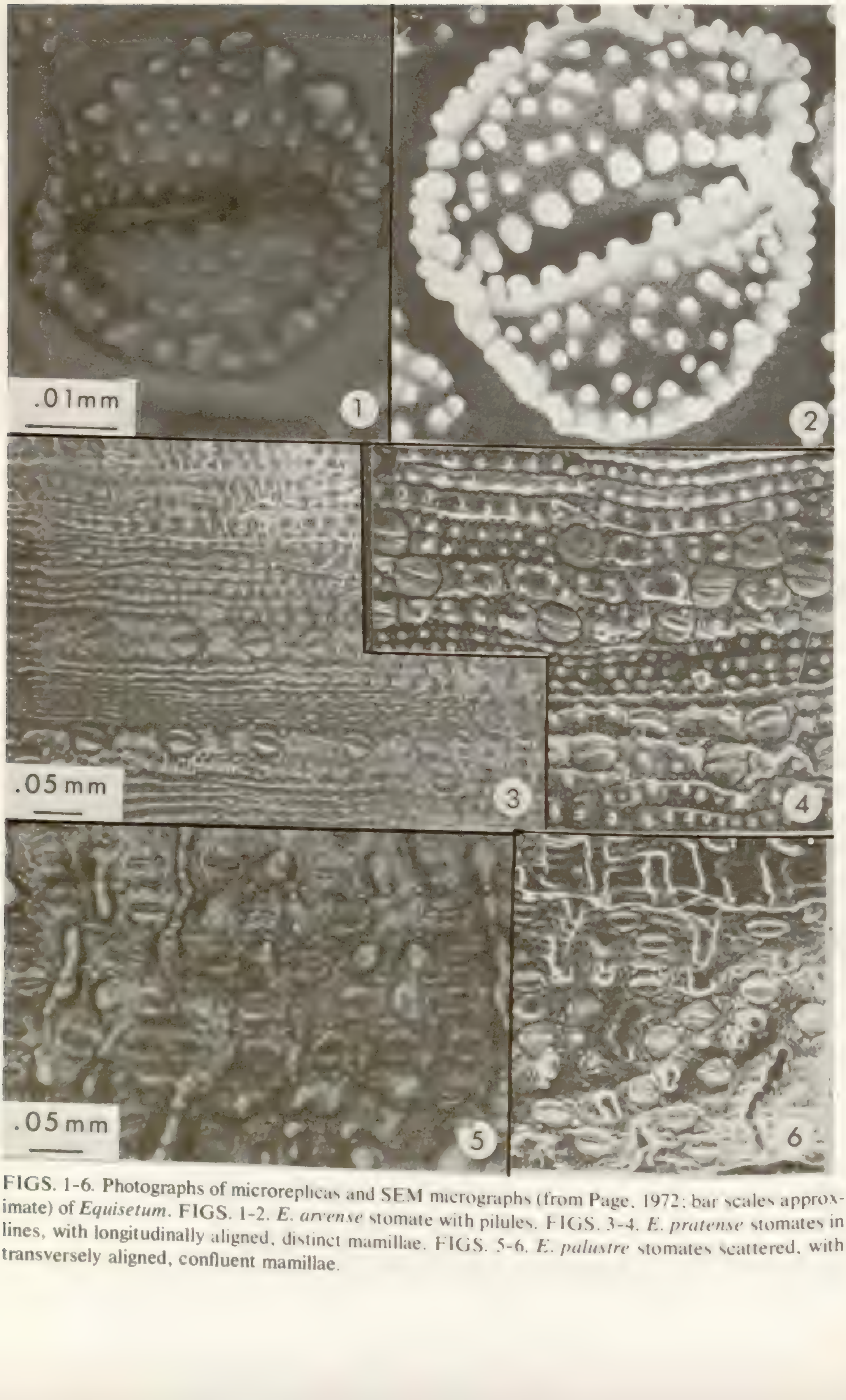

FIGS. 1-6. Photographs of microreplicas and SEM micrographs (from Page, 1972; bar scales approximate) of *Equisetum*. FIGS. 1-2. *E. arvense* stomate with pilules. FIGS. 3-4. *E. pratense* stomates in lines, with longitudinally aligned, distinct mamillae. FIGS. 5-6. *E. palustre* stomates scattered, with transversely aligned, confluent mamillae.

on branches that have been flattened well and are lying against the herbarium sheet.

The portion of branch selected is wetted with acetone, and then a plastic cover slip (22 mm^2) is pressed firmly against it. One can apply maximum pressure by using the end of the thumb, pressed vertically with the weight of the body. After about ½ minute, the coverslip is removed. It is placed on a microscope slide impression side down and observed under a standard light microscope. The acetone will have softened the plastic and the pressure will have caused it to conform to the surface of the branch. Microscopic physical features of the surface will be impressed into the plastic, hence the name "microreplica."

As with any technique, certain precautions are necessary for it to work well. If too much acetone is used, some will move over the coverslip and the technician's fingerprint will be impressed into the plastic. If the surface is not reasonably flattened, only the high spots will be replicated. If there are abrupt heights and depths, the plastic will develop fine fracture lines that will obscure any replica. Care must be used in removing the coverslip from the branch, to avoid having the branch break and its surface stick to the plastic coverslip. I have found that a dissecting needle slid between the two helps to separate them. The coverslip, as it dries, often tends to bend. I immediately attach it to a microscope slide with permanent transparent mending tape to minimize this distortion.

The microreplicas produced by this technique show enough micromorphology to reveal the patterns detected with the SEM. It is true that the contrast is not so great and the resolution of finer details is often poor, but one can see the size, arrangement, and distinctness of mamillae and the type and distribution of pilules on the stomata. *Figure 1* is a photograph of a microreplica showing the stomate and pilules of *Equisetum arvense*, and *Fig. 2* is an SEM micrograph from Page (1972) of the same species. *Figures 3* and *5* are photographs of microreplicas showing the mamillae and stomatal arrangement of *E. pratense* and *E. palustre*, respectively, and *Figs. 4* and *6* are SEM micrographs from Page (1972) of the same species.

As can be seen, there are micromorphological characters useful in species identification, and these characters can be detected quickly on questionable herbarium specimens using the microreplica technique.

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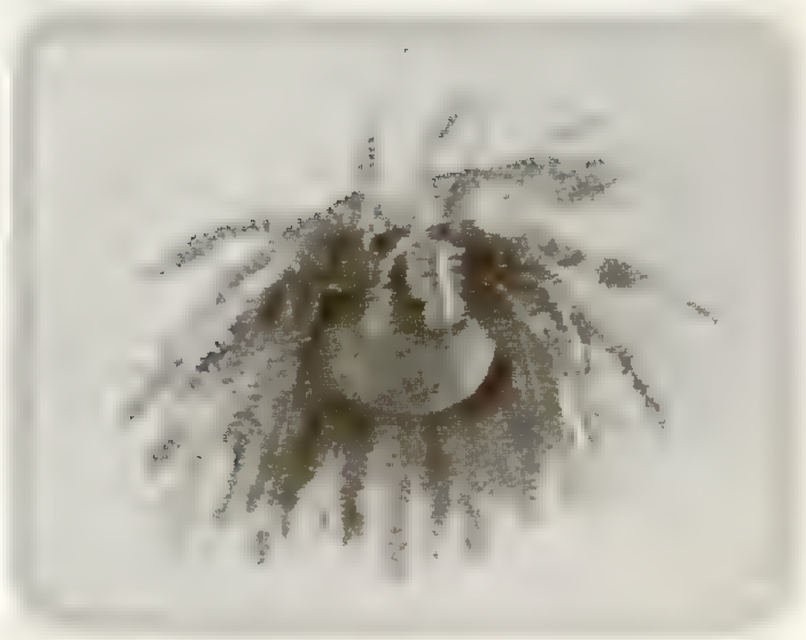

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The Establishment of Bracken Following Fire in Tropical Habitats

STEPHEN R. GLIESSMAN*

The spread of Bracken, *Pteridium aquilinum* (L.) Kuhn, as a vigorous and dominant weed is well recognized in many vegetation types throughout the world (see Braid, 1959, for a review). It has been demonstrated that this dominance is a consequence of the fern's rapid extension of underground stems and abundant vegetative reproduction (Watt, 1943, 1947), its strong allelopathic potential (Gliessman & Muller, 1972), and its resistance to fire (Vogl, 1964). Very little attention has been directed to spore germination, gametophyte formation, and sporeling establishment in relation to the dominance of Bracken.

Bracken is capable of producing large numbers of spores on each frond, and the time of spore release can extend through much of the growing season (Conway, 1957). In temperate regions, however, most spore dispersal takes place during the drier part of the year or just before the winter begins, times of the year that do not particularly favor sporeling establishment. This would explain, at least in part, reports of the small number of Bracken sporelings which become established under natural field conditions (Conway, 1953). In the tropics, where conditions of temperature and humidity are much more equable, such climatic control of spore germination and early growth presumably is less important. I have observed continual growth of new Bracken fronds throughout the year in several locations in Costa Rica (Gliessman, 1976). It is possible, then, that spore release is not restricted to a certain period, as it is in temperate regions (Conway, 1957), but may be much more haphazard over the entire year. Thus, a constant source of spores could be available for any potentially habitable area.

Observations were made in the field in Costa Rica to determine the conditions under which Bracken sporelings become established, which has possible implications for Bracken control. In Costa Rica, Bracken is encountered frequently from just above sea level on well-drained soils up to more than 3000 m elevation. As in other areas of the tropics (Richards, 1966, pp. 391-399), Bracken most often forms a type of deflected succession in regions formerly covered with dense, tropical forest. These are areas that have an annual rainfall in excess of 2500 mm, the majority of which is concentrated in the wet season that extends from mid-May to late December. Due to frequent cloud cover (especially at higher elevations) and the occurrence of sporadic rainfall even in the dry season, humidity at the soil level is quite favorable for sporeling establishment all year around.

The pattern of land use in this part of the tropics appears to lend itself quite well to the establishment of Bracken. Most forest clearing, using the well known system of "slash and burn," takes place towards the end of the wet season (December) until late in the dry season (late April). The felled material is allowed to dry as much as possible. Before the more frequent rainfall begins in early May, the slash is burned. As a consequence, when the wet season rains begin in earnest,

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the conditions that are encountered following the fire very closely approximate the ideal conditions described by Conway (1949) for sporeling establishment and young sporophyte growth. She demonstrated that spore germination took place very soon after release from the fronds, and that it was best on soils with an alkaline reaction (pH 7.0-7.7), especially on sterilized soils.

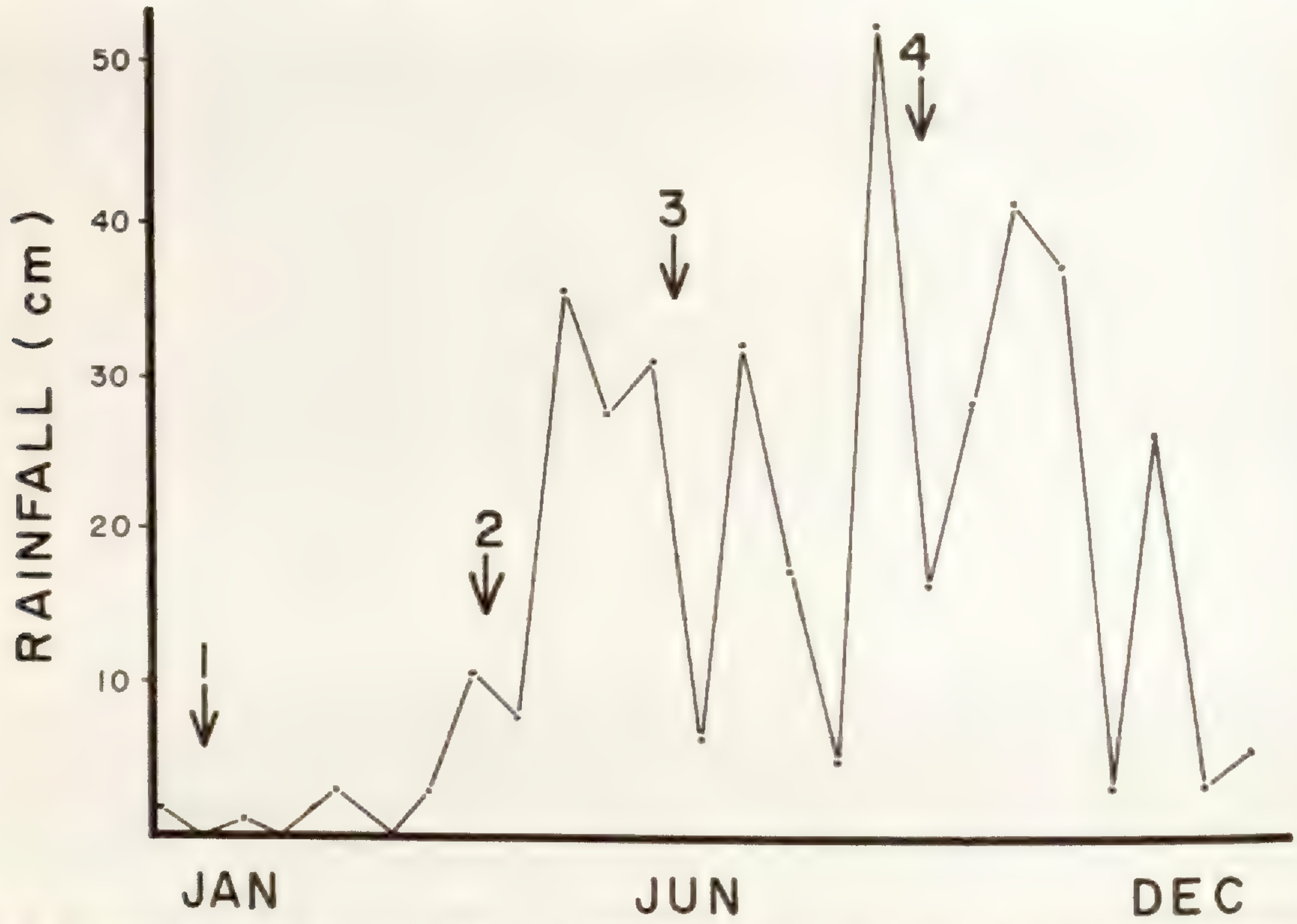

FIG. 1. Biweekly totals of rainfalls at Finca Loma Linda in 1973. 1 = initiation of forest clearing; 2 = widespread burning of slash; 3 = widespread occurrence of gametophytes; 4 = establishment of young sporophytes.

On the western boundary of Finca Loma Linda (1300 m elevation) approximately 2 km south of Cañas Gordas, Coto Brus, in southern Costa Rica, a section of montane moist tropical forest was cut beginning in the early dry season (*Fig. 1*). In late April, the slash was burned. Immediately following the first heavy rains two weeks later, I performed soil pH analyses of the upper 5 cm of soil, including the ash layer. Readings ranged from pH 7.0 to 8.0, there being a positive correlation between higher pH and greater ash depth. The ashes were compacted into a dense layer on the soil surface by the rains and ranged from 3 to 11 mm deep. Low areas and depressions where rainwater had accumulated had the greatest ash depth. In a part of the deforested area that escaped burning, I found pH readings ranging from 5.2 to 5.8, the soil surface being covered with a mat of organic matter composed of humus and intact plant detritus up to 3 cm thick. Thus, only on the burned areas after the onset of the wet season did conditions combining a high pH and a probable reduction in microbiotic diversity exist which were ideal for sporeling development.

Four weeks after the soil pH analyses were completed, on 7 June 1973, I made direct counts of gametophytes easily visible with the naked eye in ten randomly

placed, 10 cm^2 plots. I found (*Table 1*) that a considerable number of well-formed Bracken gametophytes already had become established. Coverage of the soil surface by the developing gametophytes was practically complete. Much closer inspection would probably have revealed more recently germinated spores and very young gametophytes. Nevertheless, the quantities observed are much higher than any others that have been reported in the literature for observations made under natural field conditions (Whyte, 1930; Conway, 1953). Careful inspection of those cutover areas that escaped burning failed to reveal any Bracken gametophyte establishment.

On 18 August 1973, I reexamined the same sites for the establishment of young sporophytes. Of the gametophytes originally observed, approximately 20% had formed sporophytes (*Table 1*). The number may actually be less than 20%, because individual gametophytes were not marked and new gametophytes could have developed during the time following the initial observations. Still, the numbers of sporophytes in such small areas is impressive.

TABLE 1. NUMBERS OF BRACKEN GAMETOPHYTES IN 10 cm^2 SAMPLES TAKEN 4 WEEKS AFTER SOIL pH ANALYSIS AND SPOROPHYTE ESTABLISHMENT 10 WEEKS LATER.

Sample no.	*No. gametophytes*	*No. sporophytes*
1	115	27
2	85	15
3	68	13
4	127	16
5	94	23
6	73	14
7	78	17
9	96	19
10	84	10
Average	92.2	16.9

On more favorable sites (e.g., near downed logs or burned-out stumps) several plants had produced as many as six fronds, some up to 25 cm long, but the majority had two or three fronds with an average length of 5-10 cm. If we consider that at the time of these observations there remained at least 3.5 months of additional frequent rainfall and abundant soil humidity, the growth rates of which the young bracken sporophytes are capable (Conway, 1949) would certainly allow the plants to become well established before the more difficult conditions of the following dry season arrived.

The menace posed by the vegetative spread of Bracken in many parts of the world, including the tropics, is well known (Page, 1976). The capability of Bracken to occupy large tracts of land with former agricultural value has long been observed in Costa Rica (Standley, 1937, p. 29). Once having become established, the fern is very difficult to eradicate manually or mechanically, and only the widespread application of new chemical fernicides offers control (Martin, 1976). Because of the delicate nature of gametophytes in general and the rather narrow tolerance for environmental stress of the germinating spores, I believe it would be easier to prevent the establishment of Bracken than to remove it following its introduction.

During the early stages of development, especially initial establishment, individual plants are most susceptible to adverse environmental factors. In the case of Bracken, understanding that the optimum conditions for sporeling establishment are very similar to those encountered following fire, management practices that avoid these conditions would best prevent its introduction. In the tropics, where conditions of temperature and humidity are very favorable for gametophyte establishment and growth all year around, control of soil characteristics such as pH and microbial diversity might be a positive preventive. Fire should not be used in regions especially susceptible to Bracken infestation or close to areas already dominated by the fern after the original vegetation has been cleared. If high labor cost or physical obstruction to planting caused by the downed slash makes the use of fire necessary, it could be applied only if the slash were gathered in mounds, burned, and then the concentrated ash carefully observed and clinically treated or repeatedly disturbed if gametophytes or young sporophytes appear.

Bracken rapidly takes advantage of conditions created after fire in the tropics. Young sporophytes become established in a very short time in areas where Bracken did not exist before. The widespread use of fire in the tropics thus favors an ever-increasing spread of Bracken. Observations on the establishment of sporelings following fire may provide the necessary tools for preventing dominance by this fern.

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The Distribution and Ecology of Dryopteris in Southeastern Virginia and Adjacent North Carolina[1]

DANIEL L. NICKRENT, LYTTON J. MUSSELMAN, LAURA A. PITCHFORD, and DAVID W. SAMPSON*

The pteridophyte flora of southeastern Virginia and northeastern North Carolina has received considerable study during the past century. Such notable botanists as Chickering, Palmer, Kearney, Small, Wherry, and Fernald have botanized in this region (see the literature review in Kirk et al., 1978). More recently, the Dismal Swamp and contiguous areas have been studied, and the results of these efforts have been included in the Floras published for North Carolina (Radford et al., 1968) and Virginia (Harvill et al., 1977). The genus *Dryopteris* has received special attention, for it was in 1899 that Palmer first collected *D. celsa* (Palmer) Small in the Dismal Swamp. More recent studies on the genus in the Dismal Swamp through 1973 are summarized in Wagner and Musselman (1978).

The present paper presents new information on the distribution of *Dryopteris* species and hybrids collected since 1974, not only in the Dismal Swamp but throughout the Virginia counties of Norfolk (now the City of Chesapeake), Nansemond (now the City of Suffolk), Southampton, Isle of Wight, and Surry, as well as the North Carolina counties of Hertford, Gates, Chowan, Perquimans, Pasquotank, and Camden. This is an area roughly delimited by the James River to the north, the Atlantic Ocean to the east, the Chowan River to the west, and Albemarle Sound to the south *(Fig. 1)*. This work indicates that *Dryopteris* is more widely distributed in the area than formerly thought.

Our field observations indicate that in this area *Dryopteris* species always are ecotone plants. Although they are invariably found in areas contiguous with swamps, they seldom grow in inundated sites. A description of the habitat at the study location in Gates County illustrates such a habitat best. The Suffolk escarpment rises abruptly to the west. Along the slope of the escarpment are *Pinus taeda, Liquidambar styraciflua, Fagus grandifolia, Quercus michauxii, Osmunda cinnamomea,* and *Polystichum acrostichoides.*

The wet, low area which forms the eastern boundary of this *Dryopteris* site has frequent periods of inundation, especially during the winter months. As in the well drained slopes of the escarpment, no *Dryopteris* is found in this area. Dominant tree species here are *Nyssa aquatica, Taxodium distichum, Acer rubrum, Salix nigra,* and *Populus heterophylla.* The herbaceous vegetation is characterized by *Saururus cernuus, Pilea pumila, Arundinaria gigantea, Lorinseria areolata,* and *Smilax* spp.

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The ecotone where *Dryopteris* occurs contains elements from both the escarpment and the low areas. *Nyssa aquatica*, *Acer rubrum*, and *Taxodium distichum* usually are the dominant trees. The understory consists of *Ilex opaca* and *Asimina triloba*. *Lonicera japonica* (the weedy Japanese Honeysuckle) is common throughout the swamp; however, it serves as a good indicator of a *Dryopteris* site when present with the woody plants noted above. Other ferns, such as *Athyrium asplenioides* and *Lorinseria areolata*, also are abundant here. This area has high leaf litter accumulation throughout the year, usually is damp, and receives very little light.

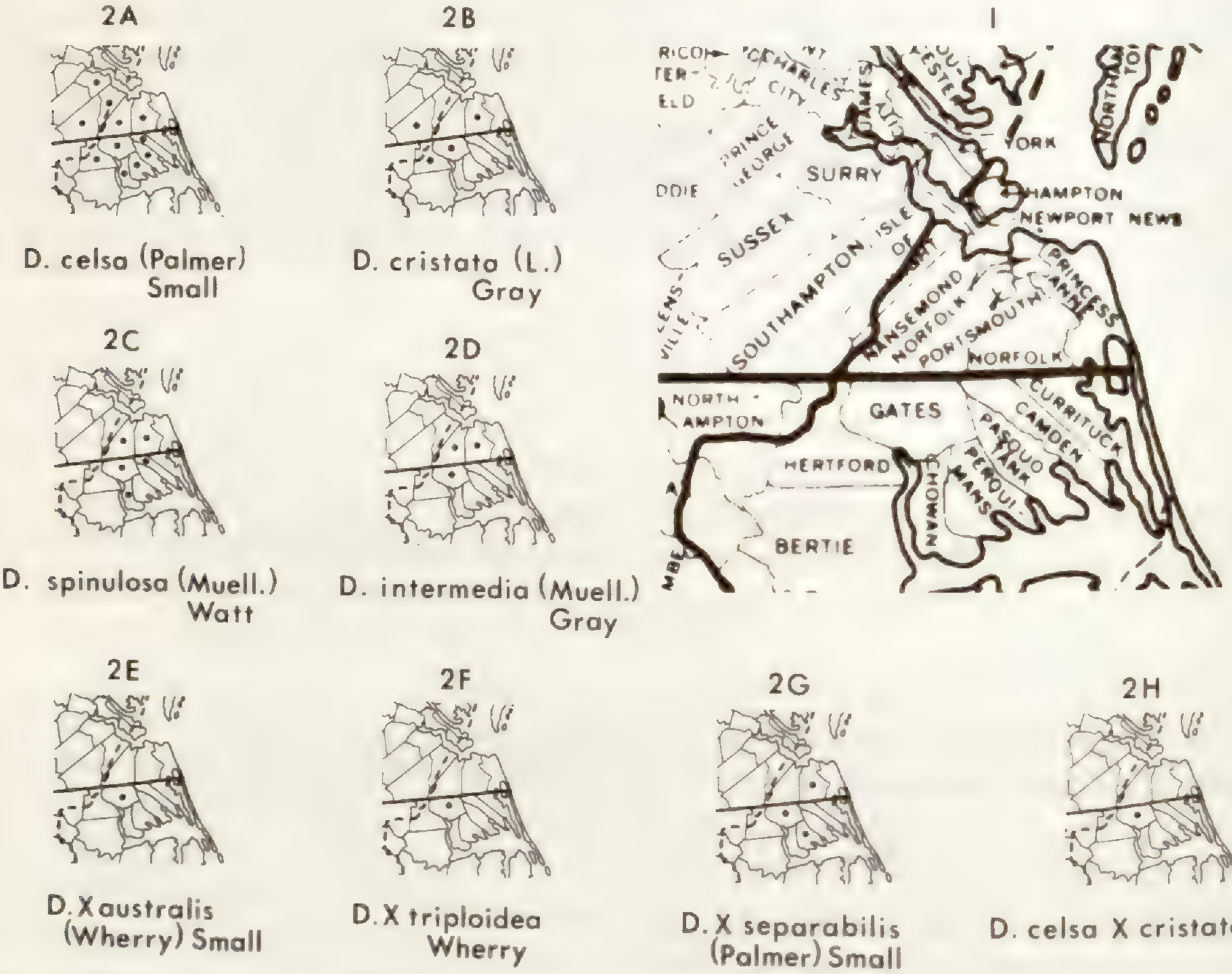

FIG. 1. County map and the study region. FIG. 2A-H. Distribution of *Dryopteris* taxa in the study area.

The center of *Dryopteris* distribution in our study region is the Gates County site, where all eight taxa found in our area occur within a few acres (*Figs. 2* and *3*). The sexual species are *D. celsa* (Palmer) Small (Log Fern), a tetraploid with the genome GGLL (see Wagner, 1971, for a discussion of this system of genome designation); *D. spinulosa* (Muell.) Watt (Spinulose Wood Fern), a tetraploid with IISS; *D. intermedia* (Muhl.) Gray (Fancy Fern), a diploid with II; and *D. cristata* (L.) Gray (Crested Shield Fern), a tetraploid with LLSS. Also present at this site are the hybrids *D* × *separabilis* (Palmer) Small (*D. celsa* × *intermedia*), ILG; *D.* × *triploidea* Wherry (*D. intermedia* × *spinulosa*), IIS; *D.* × *australis* (Wherry) Small (*D. celsa* × *ludoviciana*), GLL; and the unnamed hybrid *D. celsa* × *cristata*, GLLS.

DISTRIBUTION OF SEXUAL SPECIES

The following list summarizes the distribution of each sexual species by county *(Fig. 2)*. Voucher specimens cited in this paper are deposited in the herbaria of Old Dominion University (ODU) and the University of Michigan (MICH).

Dryopteris celsa (Palmer) Small **Figs. 2A and 3A.**

Harvill et al. (1977) listed *D. celsa* as occurring in Norfolk, Nansemond, and Southampton counties in Virginia. Two additional counties may now be added:

Isle of Wight: Two plants at margin of upland forest and small tributary of the Blackwater River, *Musselman 5055*. **Surry:** About ten plants at bottom of steep slope along small stream, *Musselman et al. 4948*.

Dryopteris celsa was described as being "rare and sporadic" and occurring no farther north than Martin County in North Carolina (Radford et al., 1968). Our field studies have shown, however, that *D. celsa* is considerably more widespread than once thought, at least in the northeastern section of the state. Recently, Hardin (1977) recorded *D. celsa* as threatened throughout all floristic provinces of North Carolina. The following list gives new county records for this fern not recorded in Wagner and Musselman (1978) or Musselman et al. (1977). In each county, the habitat is very much like the one described for the Gates County site.

Hertford: A large population of ca. 50-75 plants growing with *D. cristata, Nickrent 1271*. **Chowan:** A large population of ca. 75-100 plants growing with *D. spinulosa, Nickrent 1295*. **Perquimans:** Two small populations of less than 20 plants, one with *D.* × *separabilis, Nickrent 1298, 1299*. **Pasquotank:** Two small populations of less than 20 plants, *Nickrent 1301, 1302*. **Camden:** Many scattered populations along a creek bank; one site with four plants of *D. spinulosa, Nickrent 1278*. **Nansemond:** A population of ca. 500 plants near Whaleyville, *Musselman 4944*.

Dryopteris cristata (L.) Gray **Figs. 2B and 3B.**

Harvill et al. (1977) recorded *D. cristata* from Norfolk and Southampton counties. Efforts to find a population in the interposed Nansemond County have so far not been successful. Hardin (1977) considered this species to be threatened in the mountain and piedmont portions of North Carolina. *Dryopteris cristata* was first collected in Gates County in 1974 (*Teulings s. n.*, NCU, ODU). Since then, the Crested Shield Fern has been discovered in adjacent Hertford County *(Musselman 5472)*. Only two plants were found here among a large *D. celsa* population near Parker's Ferry. Aside from the presence of *Pinus taeda*, this habitat was generally like the ecotone described earlier.

Dryopteris spinulosa (Muell.) Watt **Figs. 2C and 3C.**

The Spinulose Wood Fern previously was known from only Cabarrus and Mecklenburg counties in North Carolina (Radford et al., 1968), until Wagner and Musselman (1978) found it in Gates County. Hardin (1977) considered this fern to be threatened in the southern Piedmont area. The range of this fern is now extended to two more counties within our study area.

Camden: About four plants among a large *D. celsa* population, *Nickrent 1274*. **Chowan:** Only two plants among a large *D. celsa* population, *Nickrent 1296*.

The rarity of this species makes the possibility of finding the hybrid between it and *D. celsa* somewhat remote. If the hybrid is to be found, however, the most probable location would be where the two parents are abundant: in the Dismal Swamp (Wagner & Musselman, 1978).

3A

3B

3C

3D

3F

3E

3H

3G

Dryopteris intermedia (Muell.) A. Gray **Figs. 2D and 3D.**

In our study area, the Fancy Fern is found in the Virginia counties of Norfolk and Nansemond and in Gates County, North Carolina. Apparently this fern has more restricted habitat requirements than the other *Dryopteris* taxa.

DISTRIBUTION OF DRYOPTERIS HYBRIDS

Dryopteris × australis (Wherry) Small **Figs. 2E and 3E.**

The postulated parents of the Southern Wood Fern Hybrid are *D. celsa* (GGLL) and *D. ludoviciana* (Kunze) Small (LL) (Wagner, 1971). To date, *D. ludoviciana* has not been collected in the Dismal Swamp area. This would be an important discovery, since only *D. celsa* is currently known to exist in the vicinity of the hybrid. In this area, *D × australis* is known only from the Gates County site. The distribution and cytology of this hybrid will be published separately (Wagner, pers. comm.).

Dryopteris × triploidea Wherry **Figs. 2F and 3F.**

Two sites in Gates County are the only known locations for the Glandular Spinulose Fern Hybrid in our study area. The rarity of the parents, *D. intermedia* and *D. spinulosa*, and the difficulty in proper identification probably account for the fact that this hybrid is seldom seen or collected. If the two parents existed together in great enough numbers, hybridization should occur, for *D. × triploidea* is common and even abundant elsewhere in its range (Wagner, 1971). For example, Montgomery (1976) mentions that this hybrid may be even more abundant than either parental species in New Jersey.

Dryopteris × separabilis (Palmer) Small **Figs. 2G and 3G.**

Previous collections of the Glandular Log Fern Hybrid have been made from Norfolk and Gates counties. A new site in Perquimans County *(Nickrent 1297)* was especially interesting, for it contained only two plants of *D. × separabilis* and only about 15 plants of one of the parents, *D. celsa*. A thorough search revealed no *D. intermedia*, the other parent. This raises the question of how plants of this "sterile" triploid originated at this site.

Dryopteris celsa × cristata **Figs. 2H and 3H.**

This hybrid is one of the more interesting fern discoveries made in the Dismal Swamp in recent years. Its genomic formula is GLLS, and the plants yield mainly sterile spores. This hybrid has been reported from only three other locations in the United States, each of which is many hundreds of miles distant from the others.

The first report of *D. celsa × cristata* was from the East Bergen Swamp in Genesee County, New York (Wagner & Wagner, 1965). The presence of aborted spores and later the recognition of 164 chromosomes confirmed the identification. In 1968, while exploring a swamp in Kalamazoo County, Michigan, W. H. Wagner and D. J. Hagenah again discovered this Log Fern hybrid (Wagner et al.,

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FIG. 3. Representative silhouettes of fronds of *Dryopteris* taxa from the study area. FIG. 3A. *D. celsa (Nickrent 1271)*. FIG. 3B. *D. cristata (Pitchford 1023)*. FIG. 3C. *D. spinulosa (Pitchford 102)*. FIG. 3D. *D. intermedia (Sampson 135)*. FIG. 3E. *D. × australis (Nickrent 1292)*. FIG. 3F. *D. × triploidea (Pitchford 2004)*. FIG. 3G. *D. × separabilis (Pitchford 2031)*. FIG. 3H. *D. celsa × cristata (Pitchford 1005)*. Bar=5 cm.

1969). The third report was by Montgomery (1975) from Bergen County, New Jersey.

In 1975, this hybrid was collected from Gates County *(Musselman 4911). Figure 3H* shows a frond of *D. celsa* × *cristata* from this site. As with most *Dryopteris* hybrids, it is intermediate in morphology between it parents.

DISCUSSION

Data presented here indicate that *Dryopteris* taxa are much more common in southeastern Virginia and adjacent North Carolina than previously was realized. Among the sexual species, one of the more significant findings of this study is the collection of *D. spinulosa* in Camden and Chowan counties, North Carolina. With the Gates County report of Wagner and Musselman (1978) and the two Piedmont counties recorded by Radford et al. (1968), the Spinulose Wood Fern is now known from five North Carolina counties.

Certainly the rarest taxon included in this study is the unnamed hybrid *D. celsa* × *cristata*. This hybrid will be given a specific epithet for consistency in referring to *Dryopteris* hybrids (Wagner, pers. comm.).The large population (ca. 100 plants) of the hybrid is located in the midst of a huge *D. celsa* stand (over 1,000 plants) and about 25 plants of *D. cristata*.

At this same site are a few scattered plants of *D. intermedia* and abundant *D. spinulosa*, yet the only *D. cristata* hybrid found here is the one noted above. We have searched carefully for *D.* × *boottii* Underw. *(D. cristata* × *intermedia)* and *D.* × *uliginosa* Druce *(D. cristata* × *spinulosa)* to no avail.

The Glandular Log Fern Hybrid *(D.* × *separabilis)* is a very rare fern, but one which will grow in disturbed habitats. We have been able to grow large numbers of sporophytes of this triploid from its "giant" spores. While we have yet to determine with certainty the chromosome makeup of either the "giant" spores or the sporophytes, it appears that spores may play an important role in the reproduction of this plant. Wagner (1971) has proposed a mechanism which he termed "hybridization by remote control," which may be an explanation for the hybrid's occurrence. This mechanism, as opposed to others, is in agreement with field observations, for the habitat of the hybrid can only be described as weedy. The plants of *D.* × *separabilis* grew along the roadside among *Rubus cuneifolius*, *Phytolacca americana*, and abundant *Lonicera japonica*. This habitat may be unfavorable for *D. intermedia* sporophytes, but adequate for the gametophytes to persist and provide the necessary gametes for hybridization. A third alternative, which we consider unlikely, is that both parents once existed at this site but only *D. celsa* persisted.

The Log Fern *(D. celsa)* has long been the most intriguing vascular plant of the Dismal Swamp, one of the few areas where it is truly common and found in large populations. Our work indicates, however, that the Log Fern is much more common in the geographical region under consideration than was realized previously. It is to be expected in well drained soil at the border between swamps and upland areas. An exception to this is its absence along any large river. This may be due to the fact that it cannot tolerate inundation. In fact, the Log Fern appears to be an

aggressive invader of disturbed areas in swamp systems. It regularly spreads to roadbanks within the Dismal Swamp. Large, vigorous plants were abundant on dredge spoils from a drainage canal at the Camden County site. Activities which impede water movement, thus making a drier habitat, favor the spread of the Log Fern. The construction of U.S. Highway 158 in Gates County apparently blocked water movement to the south, with resultant drying and the spread of *D. celsa*. Similar examples could be given from the sites noted earlier in this paper. It may be significant that of the eight county records reported in this paper, we consider only two sites (Isle of Wight and Chowan counties) to be relatively undisturbed. In these areas, *D. celsa* does not form large stands, but rather occurs scattered among plants of *Woodwardia areolata*, *Athyrium asplenioides*, and *Onoclea sensibilis*. Thus, we consider *D. celsa* to be more abundant now than at any other time in recent history.

Dryopteris celsa is morphologically quite variable within our study area. One of us (DWS) has begun a study of variability in *D. celsa* using such characters as the pinna angle in relation to the rachis and the shape of the pinnules closest to the rachis. Of particular interest is the presence of aborted and "giant" spores in morphologically typical *D. celsa* plants.

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The Fine Structure of the Newly Formed Spore of Onoclea sensibilis

NORMAN P. MARENGO and MARIE A. BADALAMENTE*

The fine structure of the dividing meiocyte of *Onoclea sensibilis* L. was described by Marengo (1977), and that of the mature spore of the closely related *Matteuccia struthiopteris* (L.) Tod. by Marengo (1973). It is of interest to establish the ultrastructure of the cells formed at the termination of the second meiotic division. Marengo (1949) reported that cytoplasmic inclusions resolvable by light microscopy apparently disappeared during spore enlargement and that proplastids and plastids made their appearance as the large vacuole was replaced by more cytoplasm. To establish the identity of cytoplasmic inclusions received from the meiocyte and to elucidate the fine structure of the young spore, an electron microscope study was made of a sporangium shown by thick sections to contain young spores just separating from the tapetum (*Fig. 1*, T).

Individual sporangia dissected from young fertile fronds were fixed in glutaraldehyde followed by osmium tetroxide and embedded in Epon (Spurr, 1969). 0.5 μm sections were cut from individual sporangia and examined by phase contrast microscopy without staining. From a sporangium identified as having spores at the desired stage, thin sections were cut with a diamond knife, stained with uranyl acetate and lead citrate, and examined with an Hitachi HU-11A EM.

Identifiable inclusions present in the young spore shown in *Figs. 1* and *2* include lipid droplets (L), amyloplasts (A), and mitochrondria (M). Small vacuoles (V) are present, as well as a loosely organized endoplasmic reticulum.

At this stage, the spore nucleus appears to have not yet reached full interphase, since a nucleolus is not present and the nuclear membrane (*Fig. 2*, NM) is poorly defined. The mature spore of this species has a nucleolus occupying fully one-third of the nuclear cross-section (Marengo, 1956).

It is hoped that the optical disappearance and re-appearance of inclusions in the enlarging spore can be followed with ultrastructural techniques. Properly buffered fixative may allow preservation of stages plasmolyzed by the fixatives of light microscopy. Older sporangia are to be dealt with in the next phase of this study.

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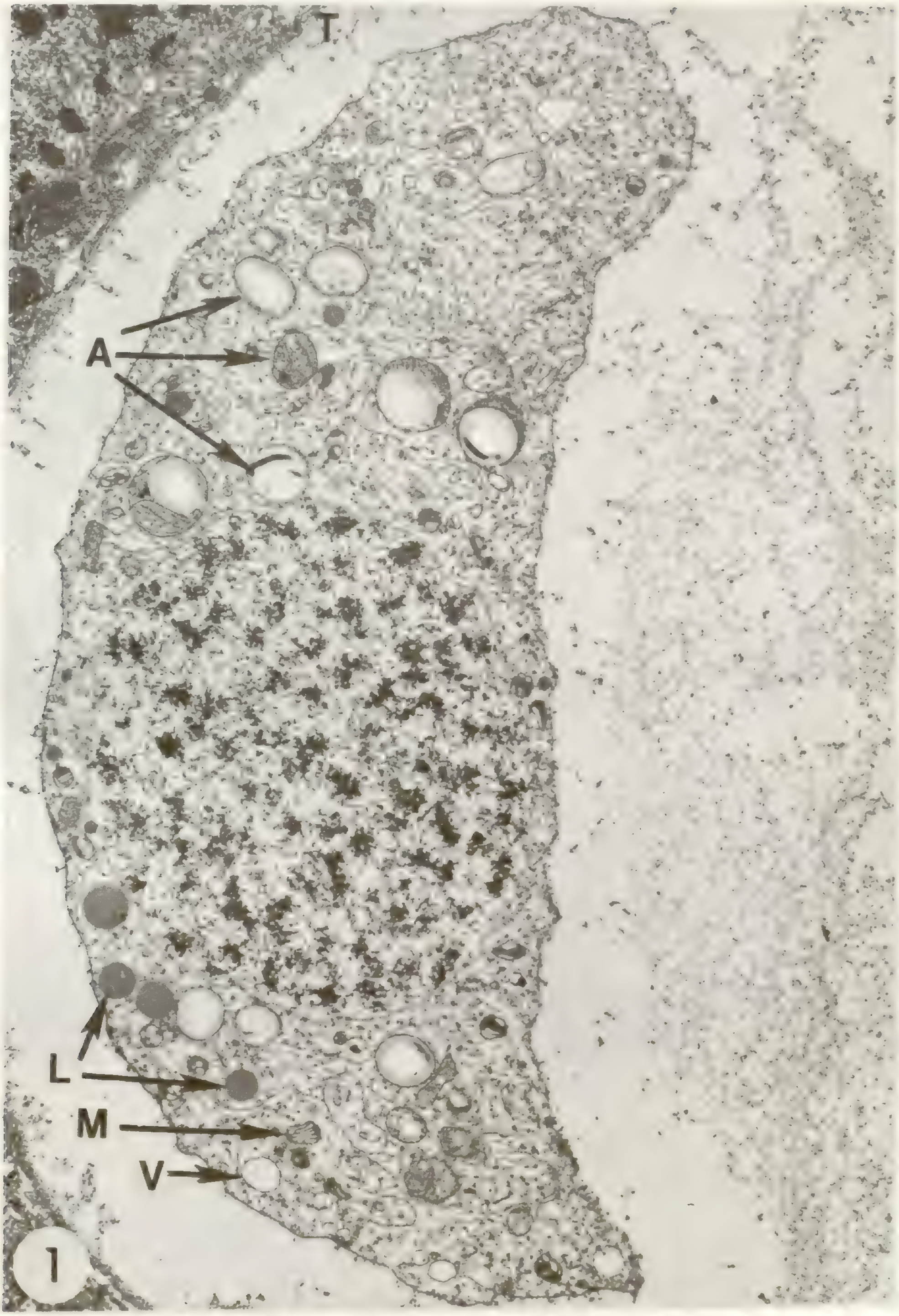

FIG. 1. Longitudinal section of a young *Onoclea sensibilis* spore, newly separated from the tapetum (T). Identifiable inclusions are amyloplasts (A), lipid droplets (L), and mitochrondria (M). Vacuoles (V) are present, and a loosely organized endoplasmic reticulum is apparent. ×11,080.

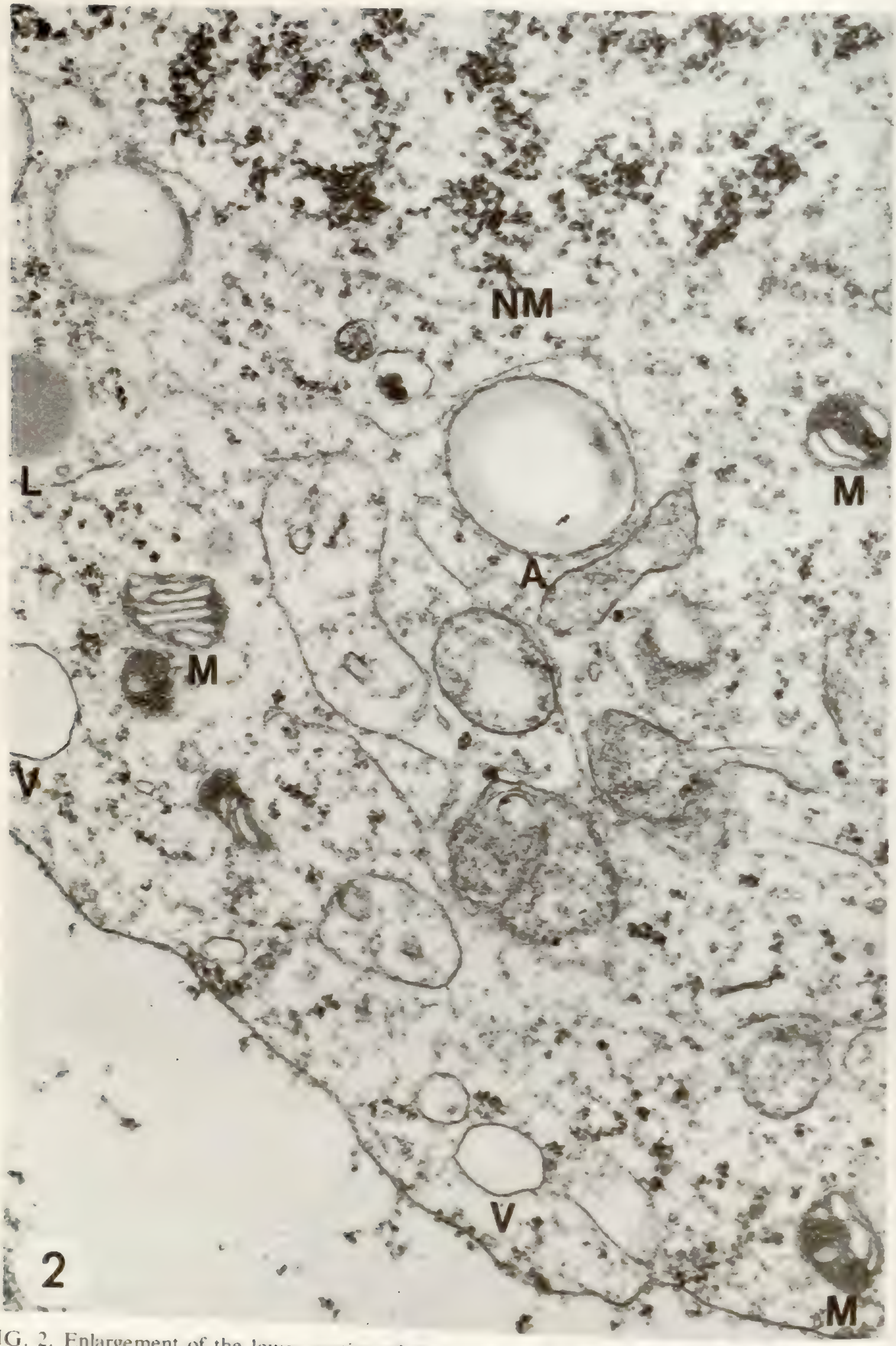

FIG. 2. Enlargement of the lower portion of the spore in *Fig. 1*. Organelles labeled as in *Fig. 1*. Nuclear membrane (NM) appears diffusely organized. Organelle adjacent to labeled amyloplast (A) is probably the surface view of a mitochrondrial crista. ×33,175.

The Anatomy of Equisetum diffusum Tubers

S. S. BIR*

Equisetum diffusum D. Don, which belongs to subg. *Equisetum* (Hauke, 1974), is characterized by similar fertile and sterile stems, and is distributed throughout the Himalayas from Kashmir in the west to Darjeeling-Sikkim and Khasya in the east, at elevations of 1,500-2,400 m. It inhabits moist, partially exposed, sandy-gravelly soil along roadsides or in ravines, and is fertile from July to September. Up to four underground tubers may be present per plant during March and April on collections made from the Dhobi ghat and Pari Tibba, at 1,500 m elevation near Mussoorie, a hill resort in the western Himalayas. Such plants were described briefly by Mehra and Bir (1959). Tubers also occur in *E. arvense*, *E. palustre*, *E. sylvaticum*, and *E. telmateia* (Campbell, 1918; Hauke, in litt.).

Although the anatomy of *E. diffusum* has been studied by Sen and Sen (1973), the tuber structure has remained undescribed until now. Material from Mussoorie was fixed in formalin-acetic acid-alcohol. Mostly free-hand transections were cut and stained with safranin and fast green.

Tubers on the rhizome appear to arise as a result of stunted growth of the lateral shoots arising from the nodes, and generally consist of one long, swollen internode. A median transection of the tuber is almost circular in outline and has a narrow zone of tracheary tissue composed of a ring of 10-12 small collateral vascular bundles embedded in a large matrix of ground tissue (*Fig. 1*). The epidermis and 2 or 3 layers of outer cortex below it consist of somewhat thick-walled cells resembling cork. Usually these are devoid of any starch (*Fig. 2*). Often some long, papilliform epidermal hairs are present (*Fig. 3*). The inner cortex consists of thin-walled parenchymatous cells densely filled with simple, globular or oval starch grains having concentric striations and a well-marked, streak-like hilum. Each vascular bundle is demarcated by its own endodermal layer, the cells of which possess the usual casparian thickening on their radial walls. This is similar to the endodermis in *E. arvense* tubers (Barratt, 1920, fig. 9). A single-layered pericycle lies underneath the endodermis. The endodermis and pericycle have denser contents, compared with those of the adjacent tissue. The metaxylem elements are placed irregularly, with a few protoxylem elements somewhat mesarch in position. The carinal canal so characteristic of the rhizome and stem of this species is lacking in the tubers. Phloem has the usual structure (*Fig. 4*). Maceration of the xylem elements revealed only tracheids.

In contrast to the endodermis position in the tubers, that in the rhizome and stem of this species shows a common ring of endodermis surrounding all the vascular bundles. In my material, the root stele is di- or triarch, with two or three protoxylem groups surrounding a single axial metaxylem element, contrary to the earlier report of triarch roots by Sen and Sen (1973).

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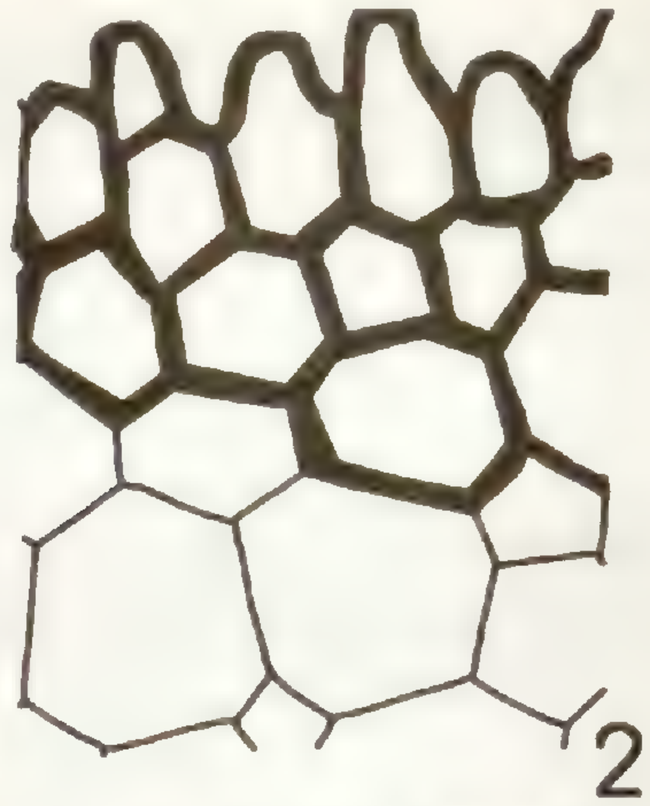
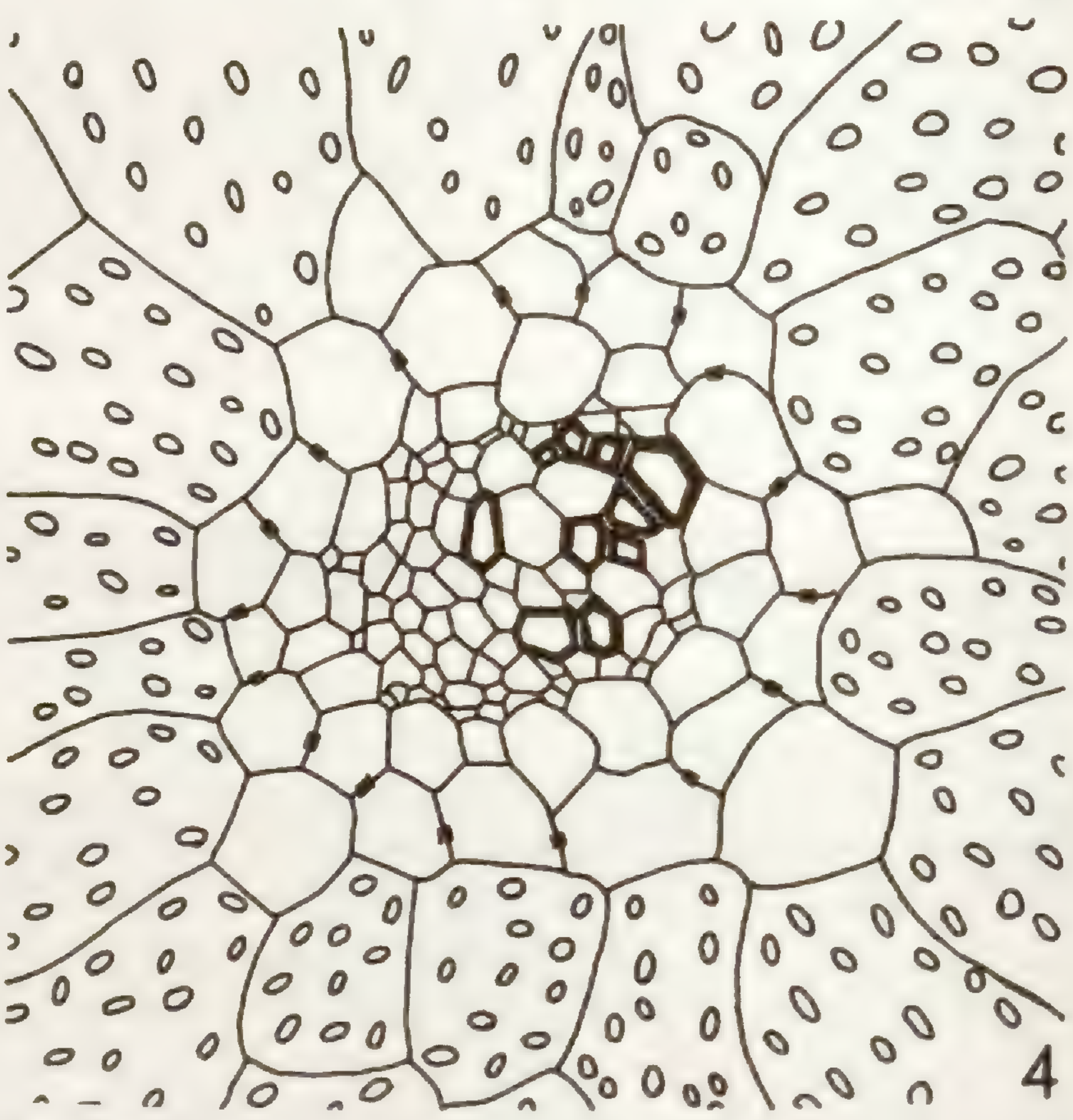


1mm
Fig. 1

0.2mm
Fig. 2 – 3

0.1mm
Fig. 4



FIGS. 1-4. Anatomical details of *Equisetum diffusum*. FIG. 1. Partial transection of tuber showing peripheral thick-walled cells and ring of vascular bundles. FIG. 2. Section of outer portion of tuber showing epidermis and cortex. FIG. 3. Long, papilliform hairs. FIG. 4. Vascular bundle and surrounding tissue of tuber.

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A New Species of Asplenium from Guatemala

ROBERT G. STOLZE*

Asplenium is one of the largest and most interesting genera of ferns in the neotropics. Many of its species are distinctive and quite easy to identify, but a few others, notably *A. auritum* Swartz, *A. cuspidatum* Lam., and *A. radicans* L., are so highly variable that intensive monographic studies will be required to define their specific and infraspecific limits. During my studies of the genus for the "Ferns and Fern Allies of Guatemala," a total of 40 species (including a number of varieties) have been recognized in this small Central American country. One of these is new.

Asplenium williamsii Stolze, sp. nov. **Figs. 1–4.**

Rhizoma erecta, paleacea; paleae lanceolatae vel lineares, fuscae, clathratae, 4-6 mm longae, 0.5-0.8 mm latae, plerumque attenuatae; folium pinnatum, 15-45 cm longum, 4-6 cm latum, ad apicem pinnatifidum vel serratum gradatim decrescens; petiolus 4-9 cm longus, plumbeus vel fuscus, anguste vel late alatus; pinnae 14-20(22)-jugae, obtusae vel subacutae, serratae vel biserratae; venae acroscopicae plerumque 1-furcatae, venae basiscopicae simplices; sori lineares, 3-8 mm longi, 0.5-0.8 mm lati, 1-2 sori proximales diplazioides.

TYPE: Terrestrial in cloud forest, Montaña Canahui, Depto. El Progreso, Guatemala, alt. 1,600-2,300 m, *Steyermark 43791* (US; isotype F).

In wet forests, commonly on the forest floor, but rarely epiphytic, 1,250-2,300 m; Alta Verapaz; Baja Verapaz; El Progreso; El Quiché; San Marcos; Santa Rosa. Mexico (Chiapas).

Plants terrestrial, rarely epiphytic; rhizome stout, erect, amply provided with lanceolate or linear, lustrous, grey-brown, clathrate scales, these 4-6 mm long, 0.5-0.8 mm broad, mostly attenuate; leaves pinnate, subcaespitose, mature ones 15-45 cm long, 4-6 cm broad; petiole stout, 4-9 cm long, much shorter than the lamina, dull grey or grey-brown, glabrous, abaxially terete, adaxially flattened and narrowly to broadly green-alate (especially toward the lamina), each of the wings 0.3-0.8 mm broad; lamina linear to narrow-elliptic, glabrous, thin- to firm-membranaceous, slightly reduced at base, gradually reduced to a pinnatifid or serrate apex, not proliferous; rachis glabrous, dull grey or reddish brown, green-alate throughout; pinnae 14-20(22) pairs, the middle ones 2-3.5 cm long, 0.8-1.5 cm broad, sessile to short-stalked, spreading to slightly ascending, approximate to subdistant, oblong to lanceolate, obtuse to subacute, inequilateral at the base, basiscopically cuneate or excavate, acroscopically truncate and often auriculate or subauriculate, the margins obtusely or subacutely serrate to biserrate; veins on the acroscopic side commonly once-forked, the basal one twice-forked, the distal ones and those of the basiscopic side simple, distinct adaxially, indistinct abaxially, the tips not or scarcely enlarged, ending well short of the margin; sori relatively long, often nearly reaching from midrib to margin (but tending to be more inframedial), linear, straight to slightly curved, 3-8 mm long, 0.5-0.8 mm broad, 1-2 proximal ones commonly double (diplazioid); indusium delicate, linear, pale yellowish to light brown, or hyaline, subentire.

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3
1
5 cm
2
4

SELECTED SPECIMENS EXAMINED:

MEXICO: Chiapas: Ridge along logging road from Las Margaritas to Campo Alegre, Municipio La Independencia, elev. 2,300 m, *Breedlove 33685* (DS, F). **GUATEMALA: Alta Verapaz:** Epiphytisch, Cobán, 1,350 m. *Tuerckheim II-1853* (US). **Baja Verapaz:** Epiphytic, broadleaf montane cloud forest, Sierra de las Minas, 3 km SE of Purulhá, alt. 1,800 m, *L. O. Williams et al. 43279* (F). **El Quiché:** San Miguel Uspantán, alt. 6,000 ft, *Heyde & Lux 3235-B* (US). **San Marcos:** On forest floor: slopes of Tajumulco Volcano, 8-10 km west of San Marcos, alt. ca. 2,300 m, *L. O. Williams et al. 26853* (F). **Santa Rosa:** Santa Rosa, alt. 4,000 ft, *Heyde & Lux 3234* (US, in part: another sheet of this at US is *A. abscissum* Willd.)

This is rather closely related to the neotropical species of *A. harpeodes* Kunze, *A. miradorense* Liebm., and *A. pteropus* Kaulf. All, in turn, form part of a larger complex of New and Old World species related to *A. erectum* Bory ex Willd., the latter reputed to be confined (at least in the strict sense) to the Old World. These taxa form a confusing tangle of species and/or varieties, which will be unraveled only when collections and types from around the world are brought together for comparison. So it is with some reluctance that I describe yet another species (albeit a distinct one), thus adding one more name to the complex.

Characters which are most useful in separating *A. williamsii* from its nearest relatives are the lustrous, grey-brown rhizome scales, which are 4-6 mm long, the conspicuously alate petiole and rachis, the relatively few (14-20) obtuse to subacute pinnae with mostly biserrate margins, veins which are commonly (acroscopically) once-forked, and the sori, most of which are very long and crowd the costa. An even more significant feature is the common occurrence of back-to-back (diplazioid) sori, which are borne usually on the basal acroscopic vein.

Asplenium harpeodes has castaneous or reddish brown scales with usually filiform tips, nonalate petioles, and numerous attenuate pinnae with mostly simple veins and marginal serrations. *Asplenium miradorense* has dull, reddish brown scales only 2-3 mm long, 20-35 pairs of pinnae, and relatively short, medial sori. *Asplenium pteropus* has the conspicuously alate petiole and rachis of *A. williamsii*, but the rhizome scales are castaneous to dark brown, the 20-30 pairs of pinnae are simply serrate and simple-veined, and the sori are relatively short and medial.

The new species is named in honor of Dr. Louis O. Williams, former chairman of the Department of Botany at the Field Museum, whose field work and publications form the backbone of the "Flora of Guatemala" project.

FIGS. 1-4. *Asplenium williamsii*. FIG. 1. Habit, × 1/2. FIG. 2. Base of lamina showing reduced basal pinnae and alate petiole, × 3. FIG. 3. A central pinna with a double sorus, × 3. FIG. 4. Portion of rhizome and cluster of scales among petiole bases, × 3.

SHORTER NOTES

A NEW LOCATION FOR PELLAEA GLABELLA IN MINNESOTA.—During July 1977, while studying pteridology under Prof. W. H. Wagner, Jr., of the University of Michigan at the University of Minnesota Biological Station, I found a new locality in Minnesota for the Smooth Cliff Brake, *Pellaea glabella* Mett. ex Kuhn. The species was discovered on July 10 and a specimen collected on July 18. A colony of five small plants was found in a precarious location at the top of a rock outcropping about 30 m above Highway 61 and overlooking Lake Superior. The locality is in Lake County, approximately two miles north of Illgen City, and about 55 miles north of Duluth. A voucher, *Weber 1*, has been deposited in the herbarium of the University of Minnesota (MIN). The northernmost station previously known for *P. glabella* in Minnesota is about 130 miles to the southwest in Chisago County between Minneapolis-St. Paul and Duluth, according to Tryon's "The Ferns and Fern Allies of Minnesota" (1954, p. 52). According to Billington's "Ferns of Michigan" (1952, p. 211), there is also a station in Ontonagon County in the upper peninsula of Michigan that is about 100 miles southeast across Lake Superior from the Lake County, Minnesota locality.—*Larry A. Weber, 415 W. St. Louis St., Pacific, MO 63069.*

SOME INSECT INTERACTIONS WITH AZOLLA MEXICANA.—It is common knowledge that ferns are not very much affected by insect predation due to the high content of chemical repellents within the plants. Still, not enough is known about the relations of ferns and insects to make this statement an invariably valid generalization. In search of examples of insect-fern interactions, I came upon a mat of *Azolla mexicana* Schlecht. & Cham. and *Lemna* sp. in the Río Potrero, Province of Guanacaste, Costa Rica, where a yellow solitary wasp, *Polybia rejecta* (F.) forma *belizensis* Cameron, was observed hovering and alighting on the *Azolla* plants, wandering about, and inserting its head among the compact leaves. When a suitable spot was found by the wasp, it went completely underwater, upturned the *Azolla*, and then searched among the roots of the fern. Capture of the *Polybia* wasp immediately after this search-submerge-catch operation brought to light an interesting case of interaction. Two genera of beetles of the family Dryopidae breed their larvae among the *Azolla* roots, which afford shelter and food for the beetles. The wasp preys on these larvae, although its diet is not restricted to them, as these wasps are rather opportunistic. Whether the Dryopidae larvae are a natural control of *Azolla* populations in this habitat is not known. But if so, *Polybia rejecta* may be responsible for controlling the Dryopid population, and thus may affect the *Azolla* population dynamics. Or perhaps the "yellow submarine" is only an occasional factor in the biology of the Dryopidae and, hence, of the *Azolla*. Apparently only one other record of submerging wasps is known, a report from eastern North America by Caudell (Proc. Entom. Soc. Washington **24:** 125-126. 1922).—*Luis D. Gómez P., Herbario Nacional, Museo Nacional de Costa Rica, Apartado 749, San José, Costa Rica.*

NOTES ON NORTH AMERICAN LOWER VASCULAR PLANTS.—Field work in Mexico and the examination of herbarium specimens at ARIZ, ASU, LL-TEX, and SRSC have revealed several new state records, a new record for the United States, and collections of apparently rare species.

Dryopteris cinnamomea C. Chr. has been found new to Texas and the United States. The collection data are: In a cave near Comstock, Val Verde Co., Texas, 980 ft elev., rare, 10 Sep 1965, *C. Babcock 100* (SRSC, 2 sheets). These specimens were filed as *Cystopteris fragilis* (L.) Bernh. The species previously was known only from Mexico (Chihuahua, Durango, San Luis Potosí, Guanajuato, Hidalgo, Distrito Federal, Morelos, and Michoacán), according to Knobloch and Correll's "Ferns and Fern Allies of Chihuahua" (1962, p. 173). I have also seen material from Coahuila.

A second known collection of *Notholaena jacalensis* Pray and one new to San Luis Potosí has been made. The collection data are: Immediately N of Minas de San Rafael, San Luis Potosí, Mexico, ca. 22°13′N, 100°16′W, growing with *Hechtia, Agave lecheguilla, Helietta parvifolia,* and *Neospringlea integrifolia* in highly mineralized soil, 1100 m elev., 30 Jun 1972, *M. C. Johnston 8178C* (LL-TEX). This species previously was known only from Jacala, Hidalgo, Mexico, according to Pray (Amer. Fern J. **57:** 101. 1967).

Pellaea breweri D. C. Eaton has been found new to Colorado. The specimen data are: Fire Lookout, summit of Roundtop Mountain, Dinosaur National Monument, Moffat Co., Colorado, in rock crevices of N-facing cliff of saddle W of lookout, 2800 m elev., 27 Jun-1 Jul 1948, *R. A. Wolf & K. S. Dever 5206* (LL-TEX). This species previously was known from Washington, Oregon, California, Idaho, Nevada, Utah, and Wyoming, according to A. F. Tryon (Ann. Missouri Bot. Gard. **44:** 138. 1957). The NW Colorado locality represents only a short range extension from Wyoming stations.

Recently I made the second known collection of *Selaginella macrathera* Weath. in I. M. Johnst. The collection data are: Chihuahua Viejo, Sierra Mapula, Chihuahua, Mexico, ca. 28°33′N, 105°51′30″W, on N-facing, rocky slopes and summit, grassland with scattered oaks, and the ledges of outcrop cliffs, 5800-7300 ft elev., 20 Jul 1977, *T. Reeves 5745B* (ASU, GH). The species was known previously only from the type collection, according to R. M. Tryon, Jr. (Ann. Missouri Bot. Gard. **42:** 42. 1955), which is about 90 mi ENE of the new station.

Selaginella leucobryoides Maxon has been found new to arizona and Nevada. The collection data are: Virgin Narrows, Mohave Co., Arizona, Sec. 32, T41N, R14W, N and E exposures on limestone cliffs and steep, rocky slopes, in desert shrub vegetation with *Larrea, Ephedra, Thamnosma, Hilaria, Ferocactus, Echinocereus, Opuntia, Galium,* and mixed with *Cheilanthes parryi,* ca. 2000 ft elev., 10 Sep 1977, *R. K. Gierisch 3983A* (ASU); and Red Rock Canyon, Spring Mountains, Clark Co., Nevada, shaded and damp N-facing cliff, 4800 ft elev., 25 Nov 1967, *V. Bostick s.n.* (ARIZ). This species was previously known only from the Providence and Panamint Mountains of SE California, according to P. A. Munz (A Flora of Southern California, p. 14, 1974). The species is apparently endemic to the mountains of the Mohave Desert. This species should be added to

the list of lower vascular plants to be expected in the New York Mountains of SE California, according to C. D. MacNeill, W. Brophy, and A. R. Smith (Madroño **25:** 54-57).

Travel was supported by NSF Dissertation Improvement Grant 77-00182 to Dr. D. J. Pinkava and the author. I thank Dr. A. F. Tryon for examining the *Pellaea* specimen and Dr. R. M. Tryon, Jr. for examining the material of *Selaginella*. I thank the curators of the cited herbaria for permission to examine their collections.—*Timothy Reeves, Department of Botany and Microbiology, Arizona State University, Tempe, AZ 85281.*

THE FERNS OF SAN SALVADOR ISLAND, II.—In the Shorter Notes of the American Fern Journal, vol. 65, p. 63, five species of ferns were reported from San Salvador Island, The Bahamas. These were *Acrostichum danaeifolium* Langsd. and Fisch., *Asplenium dentatum* L., *Nephrolepis exaltata* (L.) Schott, *Pteridium caudatum* (L.) Maxon, and *Thelypteris kunthii* (Desv.) Morton (as *T. normalis*).

Since that report, two arduous trips to the interior of the island have produced six more species not previously recorded for San Salvador Island. Five species were found in a coppice southeast of Guana Cay, the north central part of the island. The sixth species was found in the vicinity of Farquharson's plantation ruins, the southeastern part of San Salvador Island.

Adiantum tenerum Swartz was infrequent on the wall of a limestone pit in the coppice east of the mangrove swamp and southeast of Guana Cay *(R. R. Smith et al. 4072).*

Campyloneurum phyllitidis (L.) Presl was found growing around the base of *Bourreria ovata* in the coppice southeast of Guana Cay *(R. R. Smith et al. 56, 4071).*

Phlebodium aureum (L.) J. Smith was locally frequent on the upper stems of *Sabal palmetto* located along the margins of sink holes in the coppice southeast of Guana Cay *(R. R. Smith et al. 58).*

Polypodium polypodioides (L.) Watt was occasional on the bases of tree trunks in the coppice southeast of Guana Cay *(R. R. Smith et al. 76).*

Tectaria lobata (Poir.) Morton was found only once in a limestone pit just off the trail which connects Farquharson's plantation ruins to the southern end of the Great Lake. The fern was collected about fifteen feet below the surface of a thirty-foot limestone pit whose diameter was approximately eight feet *(R. R. Smith et al. 59, R. R. Smith 3947).*

Vittaria lineata (L.) J. E. Smith was occasional on the upper stems of *Sabal palmetto* located along the margins of sink holes in the coppice southeast of Guana Cay *(R. R. Smith et al. 57).*

The collections cited are deposited in the Hoysradt Herbarium of Hartwick College (HHH), Oneonta, N.Y.—*Robert R. Smith* and *Joyce E. Mauk, Department of Biology, Hartwick College, Oneonta, NY 13820.*

CHEILANTHES MICROPHYLLA, A GENUS AND SPECIES NEW TO THE BAHAMA ARCHIPELAGO.—The finding of *C. microphylla* (Swartz) Swartz on Grand (Middle) Caicos Island in the Bahama Archipelago raises to 44 the number of species of ferns and fern allies now known to occur in this region. This species also occurs in the southeastern United States, the Greater and Lesser Antilles, the Cayman Islands, and Mexico. The collection was made, in company with Ruben Sauleda and Patricia Adams, on rocks in partial shade about the mouth of caves on Village Hill, between the airstrip and Bambarra, Grand (Middle) Caicos Island, 12 Feb 1978, *D. S. Correll 49461* (F, FTG, IJ, MBG, NY, US).—*Donovan S. Correll, Fairchild Tropical Garden, Miami, FL 33156.*

THE CHROMOSOME NUMBER OF NOTHOLAENA COCHISENSIS.—Löve, Löve, and Pichi Sermolli (Cytotaxonomical Atlas of the Pteridophyta, 1977) have recorded the chromosome numbers of several species of *Notholaena*. They synonymized *N. pruinosa* and *N. integerrima* under *N. sinuata*, both of which can be separated from *N. sinuata*. These species were dealt with by Knobloch, Tai, and Ninan (Amer. J. Bot. **60:** 92-95. 1973), who stated that the chromosome number of *N. cochisensis* Goodding had not been ascertained.

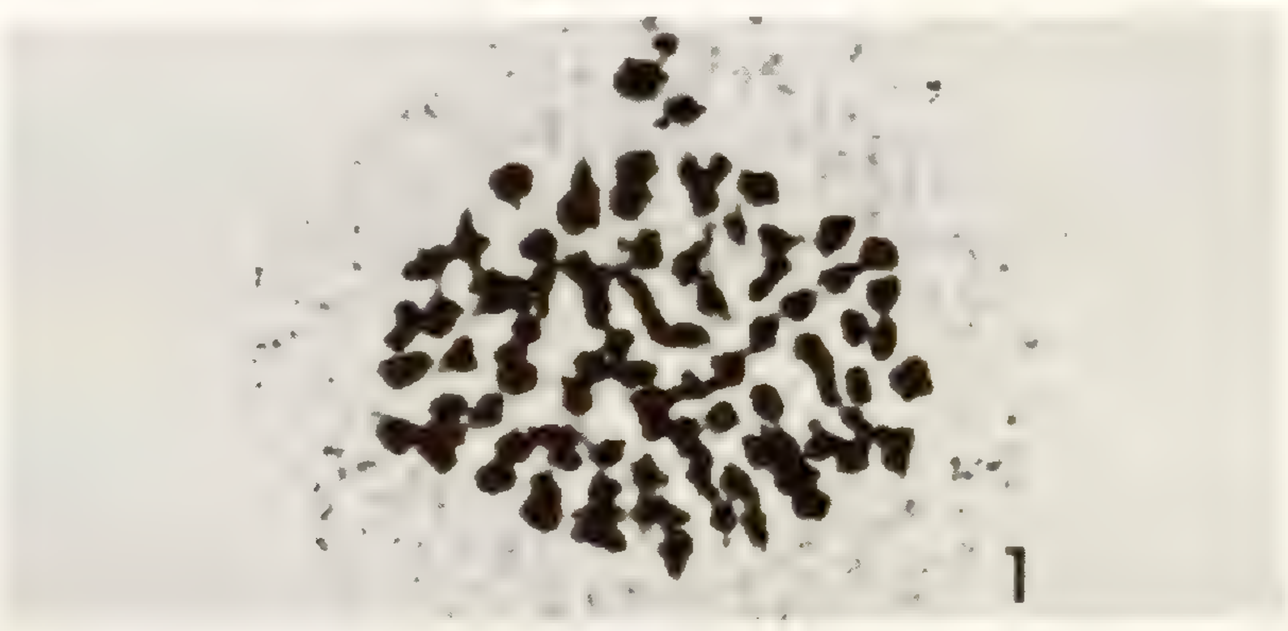

FIG. 1. Spore mother cell of *Notholaena cochisensis* (*Knobloch 2523*, MSC) at meiosis with about 87 bivalents, × 1666.

In 1977 we obtained a meiotic count shown in *figure 1* of about 87 bivalents in a triploid plant of *N. cochisensis* collected in 1973 from McKelligan Canyon within the city limits of El Paso, Texas (*Knobloch 2523*, MSC). This plant had no more than 32 fertile spores in each sporangium and presumably is apogamous. The sporophytic number should be the same as the gametophytic number, as is the usual case in apogamous ferns. According to Foster and Gifford (Comparative Morphology of Vascular Plants, 1974), 32-spored sporangia may arise in at least three ways (two meiotic and one mitotic), but the type involved here is not known.

Traditionally, the nearest relatives of *N. cochisensis* are *N. sinuata*, *N. integerrima*, and *N. pruinosa*. All of these are apogamous triploids and have $n=2n=87$ chromosomes. Whether these plants are hybrids between extant or extinct species cannot be stated with certainty until such hybrids have been synthesized. We thank Dr. Donald M. Britton for confirming our opinions.—*Irving W. Knobloch and William Tai, Department of Botany and Plant Pathology, Michigan State University, East Lansing,* MI 48823.

REVIEW

"THE PTERIDOPHYTE FLORA OF FIJI," by G. Brownlie. J. Cramer, Postfach 48, D-3301 Lehre, Federal Republic of Germany. 1977. 397 pp. DM 200.—The value of this new pteridophyte flora is threefold. It draws upon a considerable amount of recent field work in Fiji by the author himself, it updates the preceding account of Fijian pteridophytes by Copeland (1929) which appeared just before the explosion of taxonomic and nomenclatural modification in pteridophytes that continues today, and it complements the pteridophyte floras of Samoa (Christensen, 1943) and New Caledonia (Brownlie, 1969), which lie on either side of Fiji.

The work provides keys, descriptions, ecological information, line drawings, etc.; there are 32 new species or names and many range extensions and reinterpretations. Altogether it makes a very handsome volume and must be rated as a substantial contribution to pteridology.

Unfortunately it is not a polished work, although it would only have required a relatively small additional investment of effort to make it such. The introduction is inadequate, lacking any tabulation of species or novelties, any phytogeographic information and analysis, and any general account of the vegetation. The area of the flora is not clearly delimited; Rotuma Island, at least politically part of Fiji, is ignored.

The treatment of *Selaginella* is admittedly tentative and incomplete. *Marsilea* is omitted, although it was collected in Fiji by Horne according to Baker. An additional species is *Pronephrium asperum* (Presl) Holttum, represented by *Gillespie 3880* (MICH).

A varietal name is elevated to replace the legitimate *Dennstaedtia intermedia*, despite the fact that names have no priority outside their rank. *Dryopteris maxima* is transferred to *Arachniodes* while *D. subarborea* is maintained in *Dryopteris*, although the two are so closely related that Christensen opined they were only geographic variants. The separation of *D. maxima* is based solely on what in this species complex is an unstable aspect of frond architecture and which in no way demonstrates a relationship with *Arachniodes*.

The new species *Bolbitis vanuaensis* Brownlie appears to be *B. quoyana* (Gaud.) Ching, judging by Hennipman's monograph of the genus (1977). The new species *Grammitis stipitata* Brownlie is a later homonym of *G. stipitata* Proctor (1966). Several nomenclatural corrections already on record were overlooked. The revision of Pacific Thelpteridaceae by Holttum (1977) also renders Brownlie's account obsolete in places, and doubtless other changes will have to be made as revisionary work proceeds on "Flora Malesiana."

Brownlie's major error was choice of publishers. The time has come for authors to abandon the profit-gouging, high-overhead western European technical publishers and to print their works locally instead. At approximately $100 in U.S. funds, I feel that no individual pteridologist, botanist, or Fijian should make the purchase. The desirability of the contents is outweighed by the price, which is particularly galling because today's technology allows rapid and cheap production of printed matter.—*M. G. Price, Department of Botany, University of Michigan, Ann Arbor, MI 48109.*

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Spread of the Exotic Fern *Lygodium microphyllum* in Florida

CLIFTON E. NAUMAN and DANIEL F. AUSTIN*

Lygodium microphyllum (Cav.) R. Br. (Schizaeaceae) was first reported as an adventive in Florida about a decade ago by Beckner (1968). The plants were known to Beckner from three collections in Martin County near Jonathan Dickinson State Park and a single collection in Palm Beach County from Delray Beach. These climbing ferns should no longer be considered adventive, since they are now naturalized in both these counties. On the fringes of their range, the plants occur mostly in small clumps, while toward the center of the distribution near the Loxahatchee River and Loxahatchee Slough (*Fig. 1*), *Lygodium* may cover acres. One colony in Palm Beach County (Sect. 12, T44S, R41W) was one-quarter of a mile long and about 200 yards wide in January 1978.

In Florida, the plants are confined to wet, disturbed sites. We have found them only near canals, rivers, ditches, in disturbed swamps, and other sites which have standing water for a large part of the year.

We have not determined when the plants were introduced, although the oldest collection we have seen was made in February 1958 (*R. A. Long*, FLAS). The apparently oldest center of dispersal for *L. microphyllum* is in the Loxahatchee River area. Large and seemingly old colonies are abundant, suggesting that the plants have been there longer than the past two decades. Another, apparently younger, focal point is in southeastern Palm Beach County. Perhaps the small colony *(Fig. 1)* was started by the plants being cultivated in nurseries in the 1950's. If, as we have assumed, the ferns first became established in the Lower Loxahatchee River area, how they were dispersed upstream is unknown. Spores might have been spread accidently by birds, since young plants often appear first in small isolated patches on the margins of cypress heads.

Two other members of the genus have been reported in Florida, *L. japonicum* (Thunb.) Swartz and *L. palmatum* (Bernh.) Swartz. The former is an Asian fern naturalized from the Carolinas to Texas (Radford et al., 1968; Correll & Johnston, 1970). An old collection of *L. japonicum* in Dade County was considered to have escaped on vacant lots, but we suspect that it was only persistent from cultivation. We have not seen recent populations in southern Florida. *Lygodium palmatum* is considered a native of the eastern United States, ranging from Massachusetts to the Carolinas and Kentucky (Radford, et al., 1968). Although reported in Georgia and Florida (Small, 1938), we have seen no specimens.

*Department of Biological Sciences, Florida Atlantic University, Boca Raton, FL 33431.

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At present the two Asian species *L. japonicum* and *L. microphyllum* are well established in Florida. *Lygodium japonicum* is naturalized only in northern Florida and *L. microphyllum* only in southern Florida. Both seem to be spreading and eventually may meet. In southern Florida, *L. microphyllum* has already affected the native vegetation by smothering shrubby and herbaceous plants.

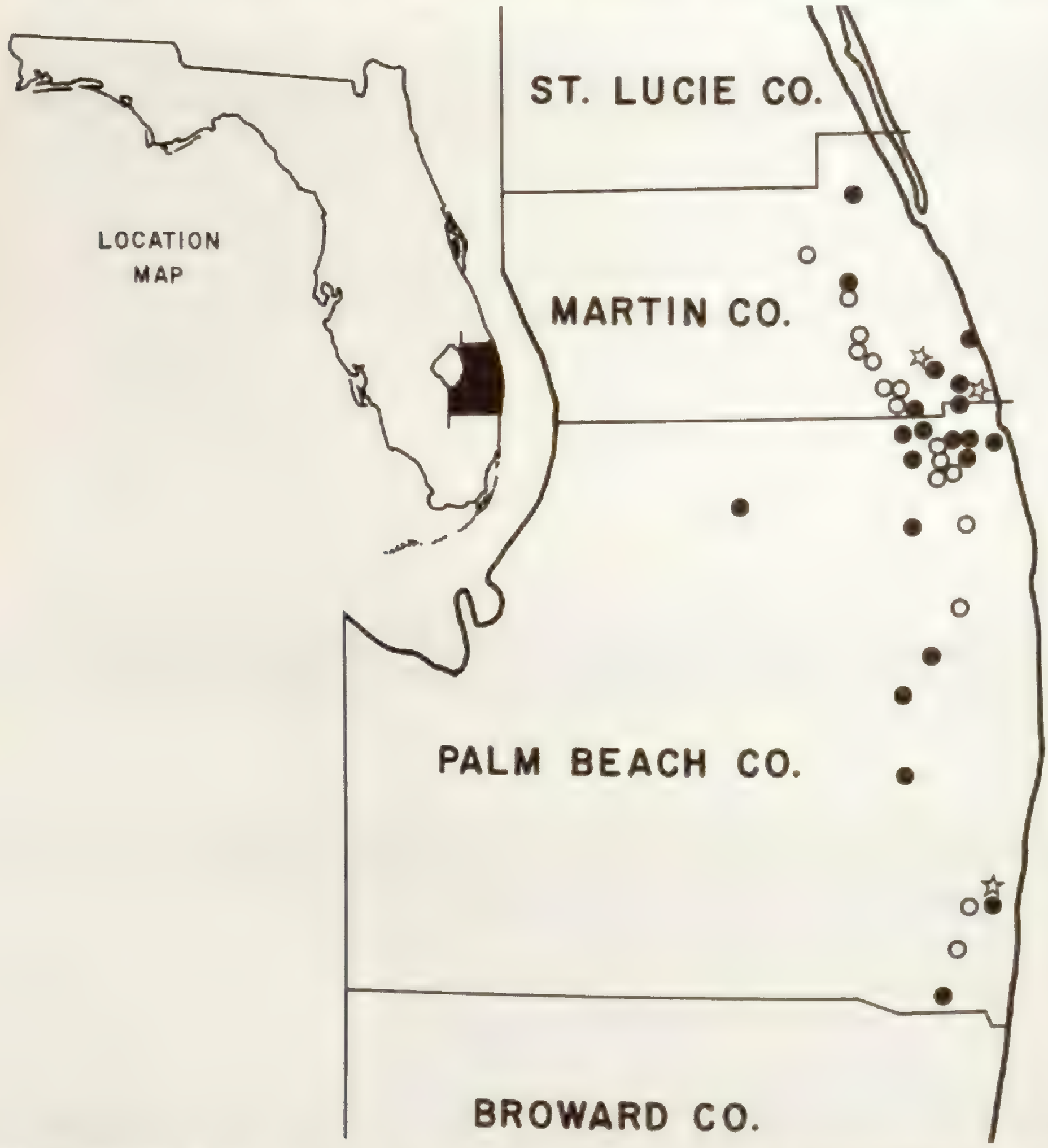

FIG. 1. Distribution of the Climbing Fern *Lygodium microphyllum* in southeastern Florida. Stars represent the points where the plants were known in the late 1960's. Dots are sites for which voucher specimens now exist. Open circles are where plants have been seen but no vouchers have been collected.

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Chlorophyll and Lipid Changes on Germination in the Non-green Spores of Thelypteris dentata[1]

ALLEN V. SEILHEIMER*

A number of morphological, biochemical, and cytochemical investigations comparing dormant fern spores with 2-celled germinated spores have been reported. Protein and lipid are the major energy reserves in dormant spores. Changes in storage protein (Towill & Ikuma, 1975), protein bodies (Gantt & Arnott, 1965), and lipid (Robinson et al., 1973; Towill & Ikuma, 1975; Gemmrich, 1977) have been investigated during germination. However, most of these investigations have utilized a few species of taxonomically unrelated ferns which have chlorophyll-containing dormant spores (Lloyd & Klekowski, 1970). Proof of the presence of chlorophyll has been shown by the absorption spectra of intact *Onoclea sensibilis* spores (Towill & Ikuma, 1973) and by extraction of *Polypodium vulgare* spores (Robinson et al., 1973). Lloyd and Klekowski (1970) have shown that chlorophyll-containing fern spores are characterized by short viability and a relatively rapid germination rate.

A second—but much more widespread—type of fern spore, believed to be non-chlorophyllous, has remained largely unstudied. This type of spore is characterized by an absence of green pigmentation, long viability and a slow germination rate. The only evidence that non-green fern spores are devoid of chlorophyll is that they lack green pigmentation when observed in the light microscope (Lloyd & Klekowski, 1970).

This investigation was undertaken to determine if the non-green spores of *Thelypteris dentata* contain chlorophyll or lipids associated with the photosynthetic apparatus. Chlorophyll content, lipid classes, and fatty acid compositions of the dormant and germinating spores are compared.

MATERIALS AND METHODS

Fronds of *Thelypteris dentata* (Forssk.) E. St. John were collected from greenhouse-grown plants and placed abaxial surface down on paper. Spore release occurred within two hours. Spores were sifted through lens paper to remove sporangial debris. 200 mg of spores were surface sterilized with an 0.5-1% commercial bleach solution and sown on sterile, modified Knop's medium (Gantt & Arnott, 1965). Germinated spores consisting of a prothallial and rhizoidal cell were obtained in 4 days under continuous fluorescent light (ca. 1500 lux) at about 25°C.

Dormant spores weighing 200 mg, or the germinated spores derived from 200 mg of spores, were homogenized dry in a ground-glass tissue grinder for 5 minutes, moistened with water for 5 minutes, and homogenized with chloroform-

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methanol (2:1, v/v) for 5 minutes. After filtration, the residue was extracted again with 2:1 chloroform-methanol. Re-extraction of the residue with chloroform-methanol (1:1, v/v) was carried out two times to insure complete extraction of phospholipids. Filtrates were combined and purified according to the methods of Folch et al. (1957). The chloroform phase of the extract was evaporated to dryness under vacuum. Methanol was repeatedly added to the residue and re-evaporated to remove traces of water. The lipid yield of dormant spores was determined at dryness in tared glass tubes.

Thin-layer chromatography was used to identify and estimate the amounts of lipid classes present in spores. Reference compounds, solvents, spray reagents, and techniques were the same as those described by Gellerman et al. (1972). Known quantities of standards were compared with known quantities of samples (400 μg) to estimate the amounts of the lipid classes present.

Techniques used to determine the fatty acid composition of spores including saponification, esterification, preparative thin-layer chromatography of the lipids to remove pigments, and gas-liquid chromatographic analysis are described elsewhere (Gellerman et al., 1972). Results were checked against reference materials of known composition. Identifications and quantifications of methyl esters were made by measuring equivalent chain lengths and peak areas from gas-liquid chromatography.

Chlorophyll content relative to the amount of lipid present (weight per cent lipid) was determined spectrophotometrically at 652 μm (Bruinsma, 1961).

RESULTS AND DISCUSSION

The fresh dormant *Thelypteris dentata* spores contain approximately 50% lipophilic material. Most of the lipid is located in large circular lipid droplets that dominate the cytoplasm (Seilheimer, 1975). The large relative amount of tri-

TABLE 1. LIPID CLASSES AND CHLOROPHYLL CONTENT OF DORMANT AND GERMINATING SPORES OF *Thelypteris dentata*.

Lipid Classes	*Spores (% Lipid)*	
	Dormant	*Germinating*
Neutral Lipids		
Triglycerides	60%	40%
Sterols and Diglycerides (free)	—	—
Carotenes, Squalene, Wax, and Esters	—	—
Glycolipids		
Monogalactosyl Diglyceride	trace	3.5%
Digalactosyl Diglyceride	trace	2.0%
Sulfolipids	—	1.5%
Phospholipids		
Phosphatidyl Glycerol	—	0.2%
Phosphatidyl Choline	0.2%	1.2%
Phosphatidyl Inositol	trace	0.5%
Chlorophyll (weight % lipid)	—	1.1%

glycerides (*Table 1*) present in dormant spores is presumably located in lipid droplets. Triglycerides have been reported as major energy reserves in other fern spores (Robinson et al., 1973; Gemmrich, 1977), moss spores (Karunen, 1971; Gellerman et al., 1972), and certain seeds (Appelqvist, 1975).

The fatty acid of dormant spores consisted primarily of palmitic, oleic, and linoleic acids (*Table 2*). The most abundant fatty acids of spores are believed to be components of the triglycerides similar to what was reported in spores of *Polypodium vulgare* (Robinson et al., 1973) and *Anemia phyllitidis* (Gemmrich, 1977).

Traces of the glycolipids, monogalactosyl diglyceride, and digalactosyl diglyceride were detected in the dormant spores. The dormant spores also contained a trace of phosphatidyl inositol and a low relative amount of phosphatidyl choline (*Table 1*). Phosphatidyl choline has been reported in envelope membranes of proplastids (Leese & Leech, 1976) and in mitochondria (Schwertner and Biale, 1973). This finding agrees with the ultrastructural observation of proplastids and mitochondria in the dormant spores (Seilheimer, 1975).

TABLE 2. FATTY ACID COMPOSITION OF TOTAL LIPID EXTRACTS FROM DORMANT AND GERMINATING SPORES OF *Thelypteris dentata*.

Fatty Acids	*Spores (% of Total Fatty Acids)*	
	Dormant	*Germinating*
Palmitic (16:0)	18.7	20.0
Palmitoleic (16:1)	0.3	0.6
Stearic (18:0)	3.8	4.6
Oleic (18:1)	46.9	45.0
Linoleic (18:2)	28.5	27.5
γ -linolenic (18:3 ω 6)	1.1	1.2
Linolenic (18:3 ω 3)	0.2	1.8
Behenic (22:0)	trace	0.1
Arachidonic (20:4 ω 6)	0.2	0.6
Lignoceric (24:0)	trace	0.2

No chlorophyll was detected in the dormant spores of *T. dentata* (*Table 1*), nor have chloroplasts been reported in the cytoplasm (Seilheimer, 1975). Furthermore, no significant amounts of lipids associated with chloroplasts, such as monogalactosyl diglyceride, digalactosyl diglyceride, or phosphatidyl glycerol (Leese & Leech, 1976), were detected in the dormant spores (*Table 1*). Analysis of non-green spore lipids from the fern *Anemia phyllitidis* also has shown a lack of diglycerides (Gemmrich, 1977). These results differ from those reported for the dormant spore of *Polypodium vulgare*, where chlorophyll, phospholipids, and glycolipids, which are normally associated with chloroplasts, are present (Robinson et al., 1973).

Triglycerides (*Table 1*), presumably composed of palmitic, oleic, and linoleic fatty acids (*Table 2*), were also major components of the germinated spores. Similar results were reported in studies of lipid in other germinating fern spores (Robinson et al., 1973; Gemmrich, 1977). This finding suggests that large quantities of lipid reserves remain unutilized during the germination process. However, a decline in triglyceride level was observed in 12 to 15 day old, multicellular gametophytes of *Polypodium vulgare* (Robinson et al., 1973) and *Anemia phyllitidis* (Gemmrich, 1977).

Chlorophyll was present in the germinated spores (*Table 1*), as were significant relative amounts of glycolipids and phospholipids (*Table 1*) that form structural components of chloroplasts and mitochondria. Monogalactosyl diglyceride and digalactosyl diglyceride are associated with grana formation in chloroplasts

(Leese & Leech, 1976) and chloroplast envelopes (Bahl et al., 1976). Their presence is also reported in mitochondria (Schwertner & Biale, 1973). Sulfolipids are found in chloroplast envelopes, stroma, and grana (Bahl et al., 1976). Phosphatidyl glycerol is a major component of chloroplast thylakoid membranes (Leese & Leech, 1976). Phosphatidyl choline is reported in mitochondria (Schwertner & Biale, 1973) and chloroplasts (Leese & Leech, 1976). The only significant change in the fatty acid composition during germination of *T. dentata* was an increase in linolenic acid *(Table 2)*. Linolenic acid is a major fatty acid of photosynthesizing tissue and probably is a structural element of the chloroplast (Hitchcock & Nichols, 1971).

This investigation of *T. dentata* substantiates the light microscopic observations and comments of Lloyd and Klekowski (1970) that the non-green, dormant spores of ferns lack both chlorophyll and lipid compositions associated with the photosynthetic apparatus. Chlorophyll and lipid composition indicative of chloroplasts were observed after spore germination.

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Gametophytes of Botrychium multifidum as Grown in Axenic Culture

ERNEST M. GIFFORD, JR. and DOROTHY D. BRANDON*

Mature gametophytes of *Botrychium* from nature have been described for several species, including *B. dissectum* (Bierhorst, 1958), *B. japonicum* (Nozu, 1954; Nishida, 1955), *B. lunaria* (Bruchmann, 1906), *B. obliquum* (Campbell, 1921), *B. simplex* (Campbell, 1922), and *B. virginianum* (Jeffrey, 1898; Bierhorst, 1958). The gametophytes are subterranean and are tuberous or somewhat elongate to button-shaped. They vary from 1-3 mm to 5-6 mm long, and even reach 1.5-2 cm in some species. The possession of a "dorsal ridge" in which antheridia are embedded is a typical feature of all the known species. The gametophytes have an associated endophytic fungus, the presence of which presumably is essential for continued growth under natural conditions.

Botrychium spores appear to have a dormancy that is not easily overcome. To date, only the spores of *B. virginianum* (Campbell, 1895), *B. ternatum* (du Buysson, 1889), and more recently of *B. dissectum* (Whittier, 1972, 1973a) have been germinated, the last species in axenic culture.

The morphology of the *B. dissectum* gametophytes cultured by Whittier (1972) fits the description for *B. dissectum* from nature, except for the presence of the endophytic fungus. Sucrose and other additives in the medium presumably replaced the contribution of the fungus under natural conditions. The gametophytes, when sexually mature, were only a few millimeters long.

Whittier (1973a) has shown that light inhibits spore germination in *B. dissectum*. He found that a minimum of 3-4 weeks in darkness is necessary for germination to occur after eight weeks in culture. Increasing the length of the dark period increased the percentage of germination. It is interesting to note that Whittier (1973b) showed that six months of darkness were required for the germination of *Psilotum* spores.

In this paper we will describe the morphology of *Botrychium multifidum* (Gmel.) Rupr. gametophytes as grown on a defined medium in axenic culture. The gametophytes of *B. multifidum* have never been observed carefully in nature.

MATERIALS AND METHODS

Spores for the present study were obtained from a plant in a greenhouse at the Department of Botany, University of California, Davis. The specimen from which the spores were taken has been growing in the greenhouse for several years. It was identified originally as *B. multifidum* subsp. *californicum*. However, the results of a recent survey (Stevenson, 1975) have shown that leaves which fit the descriptions of two or more of the presently accepted subspecies of *B. multifidum* can occur in nature on one large, copiously branched plant (which may be more than 100 yr. old). Stevenson believes that the recognition of several subspecies of *B. multifidum* is unnecessary, and so we refer the material to *B. multifidum*.

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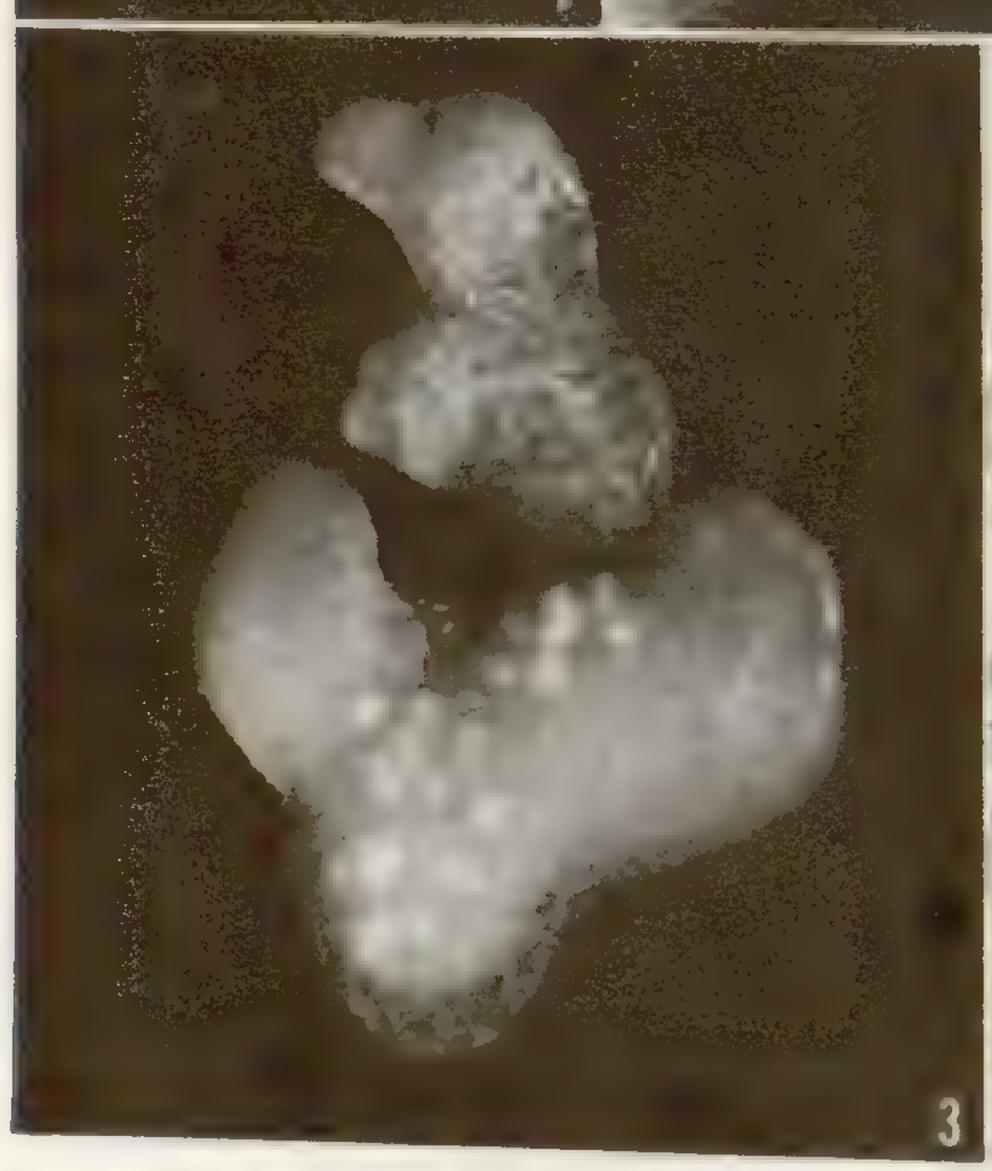
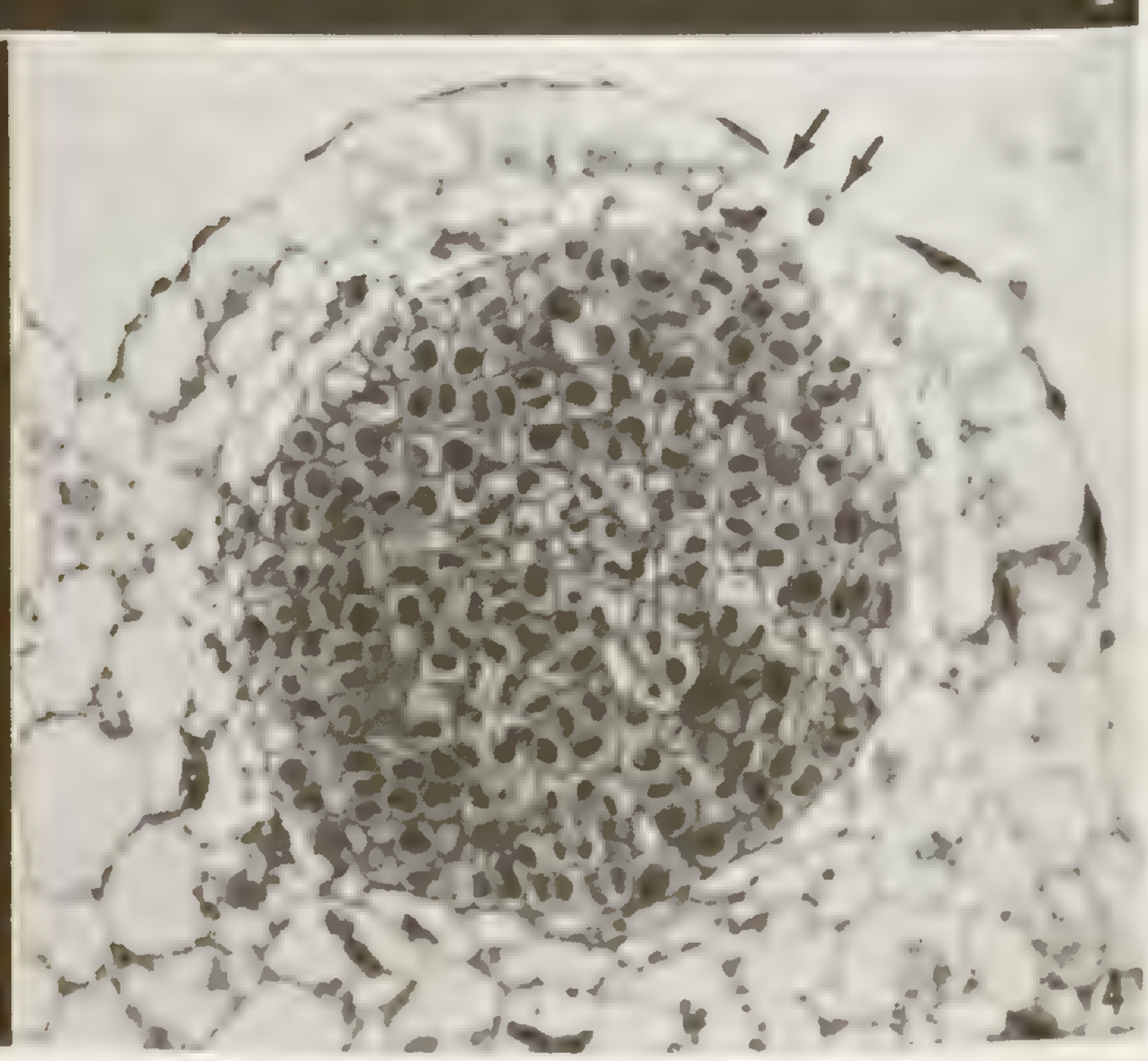
Spores were surface sterilized in 10% commercial sodium hypochlorite, washed in distilled water, and sown on a medium recommended by Whittier (1972), which is essentially that of Knudson, except that only 0.2% sucrose was added to the 0.6% agar. The pH was adjusted to 6.3. The culture tubes were plugged with





FIGS. 1-3. Various forms of *Botrychium multifidum* gametophytes grown from spores in darkness for nine months. FIGS. 1 and 3, × 15. FIG. 2, × 20. FIG. 4. Transection of antheridium from dark-grown gametophyte of *B. multifidum;* the jacket is 2 or 3 cells thick, and arrows mark two visible opercular cells, × 233.

cotton and capped with polethylene. Knowing that a minimum period of darkness was necessary for spore germination, the innoculated tubes were placed in a dark chamber. Due to an extended leave of absence of the first author, the tubes were not removed from darkness for nine months. No light-grown controls were attempted because it was known from previous experiments that the spores did not germinate in the light.

RESULTS

Numerous spores germinated during the nine months in darkness. The resulting gametophytes ranged in size from 0.25 mm to 2-3 mm; in a few cases they were 0.5 cm long. The gametophytes were generally obovoid to club-shaped, but in some instances they were irregularly branched *(Figs. 1-3)*. Rhizoids developed on the lower surface or, in some instances, only rhizoid primordia were formed. Except for the smallest gametophytes, a dorsal ridge was present upon which antheridia were embedded *(Figs. 1* and *2)*. The presence of a dorsal ridge is apparently one of the universal features of all *Botrychium* species thus far investigated. Antheridia were present on the ridge, often in groups *(Fig. 1)*, which may be the result of periodic activity of the apical meristem located at the anterior end, toward the dorsal side (Bierhorst, 1958). No archegonia have been observed, either by inspection of the surface of the gametophytes or in sectioned material. In two instances, we observed reduced, leaf-like structures (not illustrated) which may represent sporophytes, possibly of apogamous origin. In both instances, the leaves consisted of delicate petioles 1-2 cm long with reduced or abortive laminae. These were produced during the nine months that the cultures were in darkness. The leaves were dead when removed from the culture tubes. The gametophytes to which they were attached were friable, and very little information could be obtained as to the relationship or attachment of the structures. Comparable isolated, apogamously formed leaves have been found in *B. dissectum* (Whittier, 1976).

Some intact gametophytes that were transferred to fresh medium produced secondary outgrowths *(Fig. 5)*. These newly formed branches developed chlorophyll and became yellowish-green. Branching was limited and the presence of chlorophyll was ephemeral, perhaps as a result of too high a light intensity.

Gametophytes transferred to fresh medium and placed in darkness underwent an extensive proliferation of new apices from the surface of the original gametophytes *(Fig. 6)*. There was no definite pattern of branching, although in some instances the branching appeared to be dichotomous. The new outgrowths were somewhat friable and became dissociated rather easily. Antheridia developed on the dorsal side of some of the new branches.

DISCUSSION

There are no descriptions of gametophytes of *B. multifidum* from nature. Milde (1858) depicited a young sporophyte with a bulbous base; the latter structure was interpreted as a gametophyte by Clausen (1938), although Milde did not describe it as such. Stevenson (1975) searched without success for gametophytes of *B. multifidum* in several populations in the Sierra Nevada of California. In the absence of gametophytes from nature, it is difficult to know what morphological expression is representative of the species. However, the gametophytes of species already described to date share many similarities: tuberous to somewhat elongate shape, with a dorsal ridge, but varying from 1-3 mm to 0.5 cm or more long. For *B. multifidum*, perhaps the initial form of the gametophyte in culture (club-shaped with a dorsal ridge) is representative of the gametophyte in nature. Whether the

cultured gametophytes average larger or smaller than those growing under natural conditions is impossible to resolve at present.

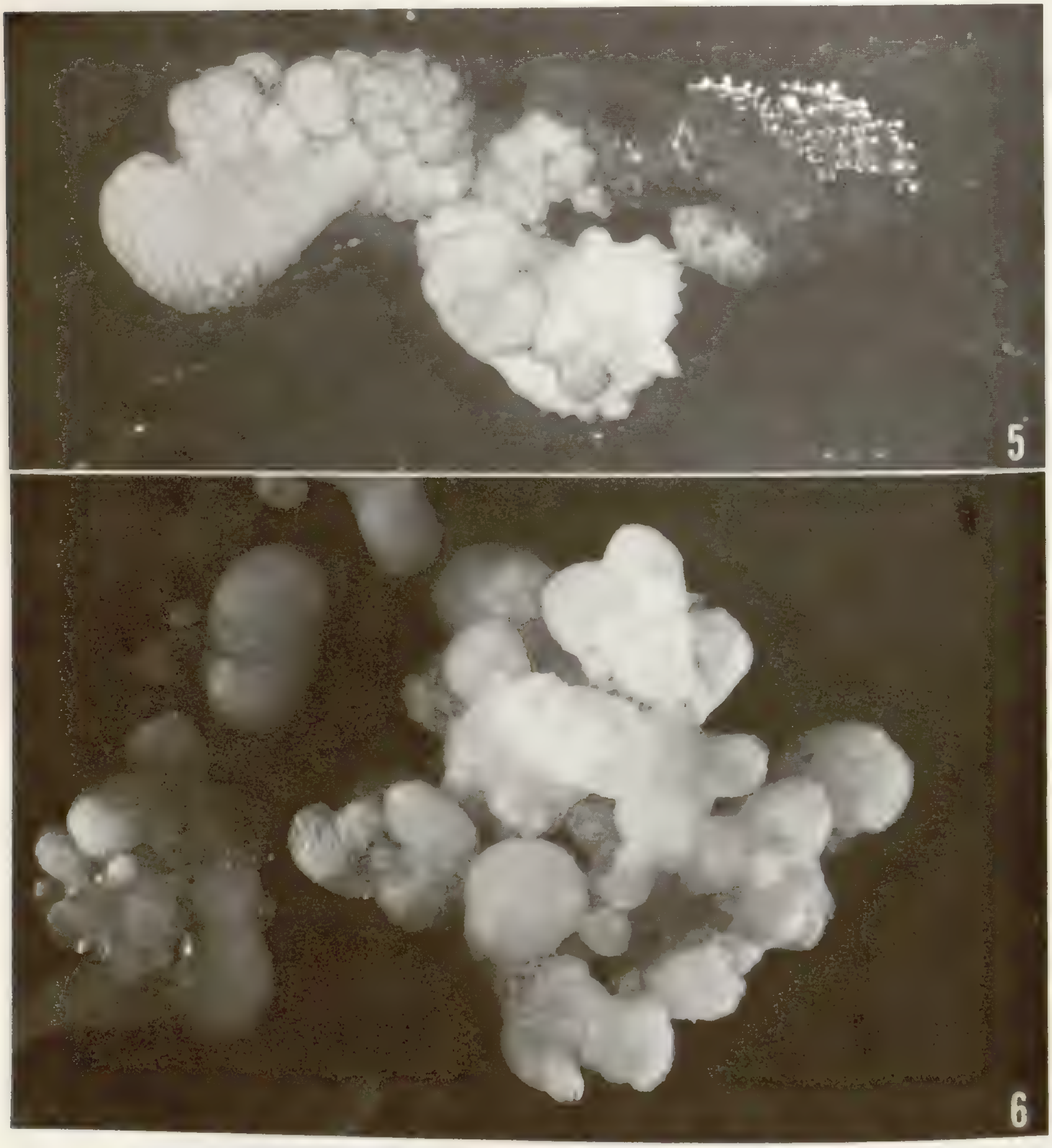


FIG. 5. *Botrychium multifidum* gametophyte initially grown in the dark, then transferred to light; yellowish-green growth produced in light appears whitish, × 12. FIG. 6. Growth produced from dark-grown *B. multifidum* gametophytes transferred to fresh medium and maintained in the dark, × 15.

It is quite possible that, in the absence of fertilization and/or apogamous development of sporophytes, the subterranean gametophytes proliferate profusely, as observed in the present study when they are grown in darkness. The clumps could be broken up through action of soil insects, worms, or even larger animals, thereby increasing the dispersal of the gametophytes. Unfortunately, such observations have not been made in nature.

In the absence of archegonia on cultured gametophytes of *B. multifidum*, one may assume that the two clusters of sporophyte-like structures were of apogamous origin.

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Revision of the Genus Cochlidium (Grammitidaceae)

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The genus *Cochlidium* was first proposed by Kaulfuss in 1820. However, the name was ignored for more than a century after its publication. Most of the species now recognized as members of the genus were included in the later *Pleurogramme* (Blume) Presl or, following Hooker (1864), were sunk into the broad concept of *Monogramma*. A detailed exposition of the generic concepts of the major nineteenth century workers would serve more to illustrate the confusion over the relationship of these ferns than to illuminate their taxonomic history. Some idea of this uncertainty can be gained by noting the number of genera to which certain of the species have been assigned.

Christensen (1929) revived Kaulfuss' name, and with characteristic care and insight provided the basis for the modern concept of the genus. He included here all the New World grammitid ferns with coenosori and one species, *C. furcatum*, with discrete, polypodioid sori. A. C. Smith (1930) later transferred another such species, *C. connellii*, to the genus. Copeland (1947), however, removed such species to the genus *Grammitis*, basing his concept of *Cochlidium* strictly on the coenosoral character.

Morton (1967) rightly deplored the artifice of Copeland's larger genera in the Grammitidaceae. His remedy was to dissolve his predecessor's genera into a single, very large genus *Grammitis*, recognizing the former groupings as equally artificial sections. From my understanding of the family, I believe that consistency with such a practice would necessitate the inclusion of all species of the family into a single genus, for none of Copeland's generic circumscriptions are without intimately related species that he included elsewhere. If a natural classification is the desired goal, the failure of another worker to define and differentiate his taxa properly is scarcely reason for their indiscriminate dissolution.

The genus *Cochlidium*, as here construed, consists of those neotropical grammitid ferns with simple and entire or at most sinuate fertile laminae, concolorous scales, hydathodes, and 2-8-celled hairs which characteristically have thickened intercellular walls and are frequently somewhat catenate. The presence of hydathodes will separate these species from nearly all those New World species of Grammitidaceae with simple fronds, and concolorous scales will remove them from many of the smaller species formerly included in *Xiphopteris*. The typical hairs are absent from the two highly derived and completely glabrous species, *C. rostratum* and *C. linearifolium*. In other species, these hairs seem to be a good indication of the relationship of some superficially quite distinct plants.

Another unifying and distinguishing feature of the genus is the stelar organization of the rhizome. Most other Grammitidaceae exhibit a fundamentally solenostelic pattern. A cross-section of the *Cochlidium* rhizome shows 1-3 vascular

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bundles, each with a straight or lightly arced row of tracheids. This contrasts sharply with the basically circular arrangement seen in most other grammitid ferns.

The presence of a coenosorus is a conspicuous feature in the genus. In most species in which it occurs, however, the coenosorus is occasionally or even frequently interrupted. On the other hand, in *C. jungens* the sori are in some plants entirely separate, although normally there is much soral fusion in most populations, occasionally to the point of forming a complete coenosorus. This shows that the coenosorus, considered an all-important generic character by Copeland and earlier authors, is not necessarily stable on even the species level. All stages leading to the compound sorus from free veins and separate sori are indicated by these variations. Also, the free receptacles of *C. serrulatum* are basal on the veins, parallel to and frequently almost fused with the costa, and are terminated by the abruptly geniculate sterile portion of the vein. This arrangement strongly suggests this species' derivation from a coenosoral ancestor.

Another character notable in the group with compound sori is the tendency of the fertile lamina to fold conduplicately over the sporangia. This feature is characteristic of certain species (*C. pumilum* and, interestingly, *C. serrulatum*), but occurs in at least some individuals of most species. My own observations in Costa Rica suggest that in *C. rostratum* folded fronds occur in plants inhabiting more stressful environments. The fronds of those species with polypodioid sori borne distally on the fertile veins seem never to exhibit conduplicate folding.

I wish to thank the staff of the U.S. National Herbarium for making this facility fully available to me, and to express my appreciation to John T. Mickel and Bruce McAlpin for their aid in my work at New York Botanical Garden. All specimens not otherwise indicated are at US.

Cochlidium Kaulf. Berlin. Jahrb. Pharm. Verbunden. Wiss. 1820: 36. 1820.

Xiphopteris Kaulf. Berlin. Jahrb. Pharm. Verbunden Wiss. **1820:** 35. 1820. LECTOTYPE: *Acrostichum serrulatum* Swartz [= *Xiphopteris serrulata* (Swartz) Kaulf.], chosen by J. Smith, Hist. Fil. 179. 1875.

Micropteris Desv. Mém. Soc. Linn. Paris **6:** 217. 1827. LECTOTYPE: *Acrostichum serrulatum* Swartz [= *Micropteris serrulata* (Swartz) Desv.], chosen by Copeland, Gen. Fil. 215. 1947.

Antrophyum sect. *Pleurogramme* Blume, Fl. Jav. Fil. 69. 1829. LECTOTYPE: *Taenitis linearis* Kaulf. [=*Pleurogramme linearis* (Kaulf.) Presl], chosen by J. Smith, Hist. Fil. 177. 1875.

Pleurogramme (Blume) Presl., Tent. Pterid. 223. 1836.

TYPE (and sole original species): *Acrostichum graminoides* Swartz [≡*Cochlidium graminoides* (Swartz) Kaulf.].

The date of the lectotypification of *Xiphopteris* is somewhat open to question. Kaulfuss erected the genus on the basis of two species, both of which had been described by Swartz in the same publication. Fée (Gen. Fil. 100. 1852) accepted Kaulfuss' genus but reduced *X. myosuroides* to synonomy with *X. serrulata*. It might be argued that since either name was available for application to his broader concept, Fée's selection of *X. serrulata* constituted implicit lectotypification. I maintain this not to be the case, as the type of neither species was excluded from

the genus. Had one name had priority, none would consider that the synonymizing of a later name constitutes typification. Alternately, if Kaulfuss had designated a type species, Fée would not have been obliged to select that name for his broader species concept. Therefore, conversely, his selecting a name should not imply the selection of a lectotype.

KEY TO THE SPECIES OF COCHLIDIUM

1. Sori compound, the receptacles linearly confluent and closely parallel to the costa.
2. Sori superficial, although at times protected by the conduplicately folded fertile lamina.
3. Fertile portion of the frond abruptly contracted in width and long-acuminate; sterile lamina usually 3 mm or more wide (West Indies, South America) .....7. *C. seminudum*
3. Fertile portion of the frond neither contracted nor acuminate; sterile lamina mostly less than 3 mm wide.
4. Sterile veins forked; midrib not evident dorsally; fronds usually 2-3 mm wide (Brazil). 8. *C. punctatum*
4. Sterile veins simple; midrib at least somewhat evident dorsally; fronds mostly less than 2 mm wide.
5. Sterile veins short, reaching less than halfway to the margin; fronds 1 mm or less wide, more than 2 cm long.
6. Fronds dichotomous (Jamaica) .....1. *C. graminoides*
6. Fronds simple (South America) .....2. *C. pumilum*
5. Sterile veins reaching more than halfway to the margin; fronds 1-3 mm wide, or if narrower than 1 mm, then less than 2 cm long.
7. Laminar margins sinuate; sterile veins somewhat evident ventrally, terminating in conspicuous hydathodes (Cuba) .....5. *C. repandum*
7. Laminar margins entire; sterile veins obscured; hydathodes present but scarcely conspicuous.
8. Midribs distinctly prominulous ventrally; laminar trichomes 2-8-celled, not clavate; fronds mostly 1.5-3 mm wide and more than 2 cm long (Puerto Rico, Dominica) ... 6. *C. jungens*
8. Midribs not prominulous ventrally; laminar trichomes 2-3-celled, the terminal cells enlarged; fronds mostly 1-1.5 mm wide and less than 2 cm long (Jamaica, Cuba) ..... 4. *C. minus*
2. Sori deeply immersed in a central groove.
9. Hydathodes conspicuous; sporangial capsules less than 250 μm long; distal annulus cells less than 45 μm high; spores less than 43 μm in diameter (widespread) .....9. *C. linearifolium*
9. Hydathodes obscure, usually not evident with 20× magnification; sporangial capsules more than 250 μm long; annulus cells more than 45 μm high; spores more than 43 μm in diameter (widespread) .....10. *C. rostratum*
1. Sori separate, round or oval, often confluent at maturity but with discrete receptacles easily visible with the sporangia removed.
10. Sterile fronds and the sterile portions of fertile fronds distinctly serrate or acutely lobed (widespread) ..... 3. *C. serrulatum*
10. Sterile laminae entire or repand.
11. Fronds 1 mm or less wide, entire, somewhat distant on slender, creeping rhizomes; stomata mostly less than 57 × 45 μm. (Venezuela) ..... 16. *C. wurdackii*
11. Fronds more than 1 mm wide or repand, tufted; stomata mostly larger than 55 × 45 μm.
12. Laminar margins provided with numerous 2-4-celled hairs (Jamaica) ..... 11. *C. proctorii*
12. Laminar margins with few or no hairs.
13. Laminae membranous, with the dark perivascular sclerenchyma of the midrib exposed dorsally; fronds usually forked; sporangial capsules, including the annulus, usually less than 140 μm long (South America) ..... 12. *C. furcata*
13. Laminae coriaceous, dorsally with midrib prominulous but covered with laminar tissue; fronds mostly unforked; sporangial capsules usually more than 140 μm long.

14. Fronds 2.5–4 mm wide, entire, mostly with 2 regular rows of sori which at maturity are not confluent across the midrib (South America) ..... 13. *C. tepuiensis*
14. Fronds 1–3 mm wide, entire or sinuate, either with sori irregularly disposed or all completely confluent at maturity.
15. Margins of the sterile laminae sinuate; fronds 1–2 mm wide (Venezuela) . 14. *C. acuminata*
15. Margins of the sterile laminae entire; fronds mostly 1.5–3 mm wide.
16. Mature sporangial capsules obpyriform, mostly 180–200 μm long; fertile laminae flat (South America) ..... 15. *C. connellii*
16. Mature sporangial capsules globose, mostly 150–180 μm long; fertile laminae at times conduplicately folded over the sori (Puerto Rico, Dominica) .....6. *C. jungens*

1. Cochlidium graminoides (Swartz) Kaulf. Enum. Fil. 86. 1824.

Acrostichum graminoides Swartz, Prodr. Fl. Ind. Occ. 128. 1788. TYPE: Jamaica, *Swartz s.n.* (S not seen; isotypes C, L–these *fide* C. Chr. 1929, BM not seen, photo and fragment at US!).

Grammitis graminoides (Swartz) Swartz, Syn. Fil. 22. 1806.

Asplenium graminoides (Swartz) Swartz, Fl. Ind. Occ. **3:** 1608. 1806.

Monogramma ? furcata Desv. Ges. Naturf. Freunde Berlin Mag. **5:** 303. 1811; *nom. nov. et superfl.* TYPE: Based on *Acrostichum graminoides* Swartz.

Pleurogramme graminoides (Swartz) Fée, Mém. Foug. **3:** 37. 1852.

Taenitis graminoides (Swartz) Mett. Fil. Lips. 27. 1856.

Monogramma graminoides (Swartz) Baker in Hook. & Bak. Syn. Fil. 375. 1868, as *Monogramme*.

Pleurogramme furcata (Desv.) J. Smith, Hist. Fil. 178. 1875.

RANGE AND HABITAT: Jamaica. According to Proctor (1953), this species occurs locally on the eastern slope of the John Crow Mountains, at elevations of 2000–3000 ft.

Proctor's collection represents the only reported gathering of this species in this century. It is otherwise known only from Swartz's original collection and from a few plants collected by James Wiles around the turn of the nineteenth century. As I have not seen the Proctor plants and since the few specimens available to me are fragmentary, I have little to add to Christensen's (1929) account of this species. However, it should be noted that despite the implication to the contrary in Christensen's key, the fertile lamina is at times conduplicately folded over the sori.

SPECIMEN EXAMINED:

JAMAICA: "Near the top of the blue-mountain," *Wiles* (BM not seen, K not seen, photo US, US!).

2. Cochlidium pumilum C. Chr. Dansk Bot. Ark. 6(3): 19. 1929.

TYPE: Chuquiribamba, Ecuador, 9 Sept 1868, *Massee s.n.* (K not seen).

RANGE: Colombia, Ecuador, Bolivia, Brazil.

Although I have not seen the type, the collections cited closely match Christensen's description. The species seems to be rare, but is clearly wide-ranging.

I agree with Christensen that this species must be very closely related to *C. graminoides*, but the discovery of additional material reinforces the assumption that the two are distinct. *Cochlidium pumilum* generally exhibits unforked fronds and strongly conduplicate fertile laminae. Also, judging from the material seen, the coenosorus is often interrupted in this species, but is rarely so in *C. graminoides*.

SPECIMENS EXAMINED:

COLOMBIA: *Acosta-Arteaga 689* (NY). **BOLIVIA:** New Brazil, 5500 ft, *R. S. Williams 1171*. Songo, *Bang 907B* (NY, US). **BRAZIL:** *A. Richard* in 1834 (NY).

3. Cochlidium serrulatum (Swartz) L. E. Bishop, comb. nov.

Acrostichum serrulatum Swartz, Prodr. Fl. Ind. Occ. 128. 1788. TYPE: Jamaica, *Swartz s.n.* (S not seen; isotype US!).

Grammitis serrulata (Swartz) Swartz, J. Bot. (Schrader) **1800**(2): 18. 1802.

Gymnopteris serrulata (Swartz) Bernh. Neues J. Bot. **1**(2): 48. 1805.

Asplenium serrulatum (Swartz) Swartz, Fl. Ind. Occ. **3:** 1607. 1806.

Xiphopteris serrulata (Swartz) Kaulf. Farrnkr. 87. 1827.

Micropteris serrulata (Swartz) Desv. Mém. Soc. Linn. Paris. **6:** 217. 1827.

Micropteris orientalis Desv. Mém. Soc. Linn. Paris **6:** 217. 1827.

TYPE: Mascarene Islands, without collector (presumably P not seen).

Polypodium serrulatum (Swartz) Mett. Fil. Lips. 30. 1856, *non* Swartz, 1802, *nom. illeg.*

Xiphopteris extensa Fée, Mém. Foug. **11:** 14, *t. 19, f. 3.* 1866. TYPE: Guadeloupe, *L'Herminier* in 1864 (presumably RB or P not seen).

Xiphopteris orientalis (Desv.) Fourn. Compt. Rend. Hebd. Séances Acad. Sci. **81:** 1140. 1875.

Polypodium duale Maxon, Contr. U.S. Natl. Herb. **16:** 61. 1912, *nom. nov.* TYPE: Based on *Acrostichum serrulatum* Swartz.

Xiphopteris auyantepuiensis Vareschi, Fl. Venez. 1(2): 879. 1969. TYPE: Auyán-tepuí, Edo. Bolívar, Venezuela, 1800 m, *Vareschi & Foldats 4806* (VEN not seen). ISOPARATYPE: Auyán-tepuí, Edo. Bolívar, Venezuela, 1800 m, *Vareschi & Foldats 4813* (US!).

RANGE AND HABITAT: Ranges throughout the West Indies and from the Mexican state of Puebla south to Bolivia. In the Old World it is known from the wetter parts of tropical Africa, Madagascar, the Mascarene Islands, and Amsterdam Island. Epiphytic and epipetric on mossy rocks. It is most frequently encountered at altitudes of 500–1500 m.

Cochlidium serrulatum is probably the most common species of the family in the New World. In spite of its small size, it is one of the most abundant in collections, and no species has a wider range. As is often the case with widespread species, considerable variability can be detected within the taxon as it is generally circumscribed. However, to date no one has successfully demonstrated the distinctiveness of any proposed segregates.

The type of *Micropteris orientalis* is uncertain. However, a collection in the de Jussieu herbarium at Paris (Ile de France et Bourbon, *de Petit Thouars s.n.* in 1808 (photo US) may represent an isotype at least. But in any case, no Indian Ocean specimens I have seen warrant taxonomic distinction on the basis of the characters that have been studied.

I suspect that Fée described *X. extensa* because he had previously confused Swartz's *Acrostichum serrulatum* with the same author's *Polypodium myosuroides* and had combined the two names under *X. serrulata* (Swartz) Kaulf. He therefore provided a new name for the concept of the present species. Although I have seen no type material of *X. extensa*, Fée's illustration is as usual quite good and leaves little doubt as to the application of the name.

The original description of *X. auyantepuiensis* Vareschi was based on two collections. No type was selected, and so the name remained invalid until the publication cited above. The duplicate of the paratype at US seems well within the range of variability of the species as a whole. Vareschi emphasized the dimorphic fronds to characterize *X. auyantepuiensis*. But in most specimens of *C. serrulatum*, the sterile fronds are shorter and more deeply lobed than the fertile ones.

In considering the morphological plasticity of this species, it should be pointed out that Walker (1966) indicated his Jamaican sample of the species to be an apogamous tetraploid. This account alone is sufficient to suggest that such a wide-ranging and variable taxon might be biosystematically complex. It would not be surprising if a carefully detailed study demonstrated that our present "species" consisted of two or more cryptospecies and hybrids between them.

To transfer the type species of a genus so well-known as *Xiphopteris* demands more than ordinary justification. Copeland (1947, 1952) strongly emphasized the restriction of the sori to a distal, nearly entire portion of the lamina in proposing an intimate relationship of *X. serrulata* with *X. myosuroides* and related species. But as I have discussed elsewhere (Bishop, 1974), laminar dissection is a weak character for the determination of species relationships in the Grammitidaceae. The *X. myosuroides* group shows clathrate scales, a solenostelic rhizome and a peculiar type of foliar trichome very different from that of *C. serrulatum* or other species of *Cochlidium*. In addition, the sori are merely impressed into the fertile lamina; the laminar margins are never conduplicately folded around the soral region. The necessary nomenclatural adjustments for the species normally included in *Xiphopteris* are being made elsewhere.

Aside from the conspicuously serrate or serrate-lobate fronds, *C. serrulatum* differs further from the other species of *Cochlidium*. The rhizome is relatively long-creeping with somewhat distant fronds, a character found otherwise only in *C. wurdackii*. The 2-4-celled laminar hairs are unusual in the genus in that the terminal cell is considerably elongated and the intercellular walls are somewhat less thickened. These trichomes seem to be nearly or quite lacking in many specimens. The hydathodes are much less conspicuous than in other species. In fact, they have been visible to me with certainty only in microscopic preparations. As they frequently are not situated over the terminus of the veins, the hydathodes may be vestigial in this species.

In view of the distinctiveness of this species, it might reasonably be retained in its own monotypic genus. However, since it is clearly related to the other species of *Cochlidium*, I prefer to include it here. But in any case, I feel sure that *C. serrulatum* cannot be retained justifiably in any generic concept which includes other species usually referred to *Xiphopteris* unless the entire family be construed to constitute a single genus.

One specimen from Venezuela merits special mention (*Steyermark & Nilsson 264-A*). This plant reveals its affinity to *C. serrulatum* through its elongate rhizome and the low serrations on some of the leaves. Other fronds, however, are quite entire. More significantly, the fertile lamina is scarcely expanded or condupquite and is conspicuously narrower than the mature sori. These characters remove the plant from the usual range of variation of the species and suggest possible hybridization with one of the Venezuelan species with polypodioid sori.

REPRESENTATIVE SPECIMENS EXAMINED:

CUBA: Oriente: Sierra Nipe, near Woodfred, 450-550 m, *Shafer 3432*. **HAITI:** Massif du Nord, Anse-à-Foleur, top of Morne Colombeau, 900 m, *Ekman H4368*. **DOMINICAN REPUBLIC:** Loma de la

Sal, Jarabacoa, 1100 m, *Liogier 11356*, 1100-1400 m, *Liogier 11691*. **JAMAICA: Portland:** E slope of John Crow Mountains ca. 5 mi SW of Priestman's River, *Proctor 4294*. **PUERTO RICO:** Serra de Naguabo, Monte El Duque, *Shafer 2246*. **ST. KITTS:** Slopes of Mt. Misery, *Britton & Cowell 500*. **NEVIS:** Nevis Peak, 900-1095 m, *A. C. Smith 10552*. **MONTSERRAT:** Top of Chaners Mountain, 3000 ft, *Shafer 292*. **GUADELOUPE:** Bains Jaunes, 700 m, *Questel 1797*. **DOMINICA:** Lower slope of Morne Micotrin, Laudat, 700 m, *Hodge & Hodge 2095*. **MARTINIQUE:** Calebasse, Deux Choux, *Duss 1609*. **ST. LUCIA:** Vicinity of Mt. Gimie, ca. 1500 ft, *Webster, Ellis & Miller 9416*. **ST. VINCENT:** Soufrière, 2400 ft, *Eggers 6709*. **GRENADA:** Vicinity of Grand Etang, 1600-1800 ft, *Proctor 17049*. **TRINIDAD:** *Fendler 81* in 1877-78.

MEXICO: Veracruz: Zacuapan, *Purpus 3021*. **Puebla:** Barranca below Honey Station, *Pringle 13853*. **Oaxaca:** Dto. Teotitlan, Mun. de Tenango, First half of trail from S. Martín Caballero to Tenango, 4300-5000 ft, *Hallberg 1437*. **Chiapas:** Mun. de Ocosingo, near Laguna Ocotal Grande, ca. 25-30 km SE of Monte Líbano, ca. 950 m, *Dressler 1641*. **GUATEMALA: Huehuetenango:** Sierra de los Cuchumatanes, vicinity of Maxbal, 1500 m, *Steyermark 48782, 48886*. **Alta Verapaz:** Cerro Sillab, Senahu, *Hatch & Wilson 169*. **Izabal:** Montaña del Mico, between Milla 49.5 and ridge 6 mi from Izabal, 65-300 m, *Steyermark 38627*. **San Marcos:** S-facing slopes of Volcán Tajumulco, along the Río Chopal, Finca El Porvenir, 1300-1500 m, *Steyermark 37465*. **Chiquimula:** Volcán Ipala, near Amatillo, 900-1510 m, *Steyermark 30511*. **BELIZE:** Mountain Pine Ridge, *Bartlett 11642*. **HONDURAS: Cortés:** Lake Yojoa, near Agua Azul, 650 m, *Williams & Molina 17877*. **Atlántida:** Lancetilla Valley near Tela, *Standley 56353*. **COSTA RICA: Guanacaste:** Vicinity of Tilarán, 500-650 m, *Standley & Valerio 44565*. **Puntarenas:** Biological Field Station at Finca Wilson, 5 km S of S. Vito de Java, 1300-1400 m, *Lellinger 807*. **Alajuela:** Near Artezalea and Methodist Rural Center, ca. 8 km NE of Villa Quesada, 550 m, *Molina et al. 17748*. **Limón:** Alto Lari, 600 m, *Jiménez M. 1888*. **Heredia:** Río Sarapiquí near Cariblanco, N of Volcán Poás, 850 m, *L. O. Williams 20246*. **San José:** Near Tarbaca, ca. 15 km S of S. José, 1900 m, *L. O. Williams 19441*. **Cartago:** Estrella, 20 mi S of Cartago, 5200 ft, *Stork 3297*. **PANAMA: Chiriquí:** Vicinity of El Boquete, 1000-1500 m, *Cornman 910, 952, 1028, 1109, 1238, 1239*. **Panama:** La Eneida, region of Cerro Jefe, *Dressler 3315*. **Darién:** Cerro Mali base camp in the Serranía del Darién, 1400 m, *Gentry & Mori 13776*.

VENEZUELA: Nueva Esparta: Island of Margarita, Juan Griego trail, 450 m, *Johnston 144*. **Aragua:** Between El Portachuela and Ocumare, *Pittier 11384*. **Falcon:** Near Santa Ana, Cerro Santa Ana, 750 m, *Steyermark & Braun 94647*. **Bolívar:** Vicinity of Upper Falls of the Río Tirica above Summit Camp, central section of the Chimantá Massif, 1940-1950 m, *Steyermark & Wurdack 531*. **Amazonas:** 1-3 km N of Cumbre Camp, Río Yatua, Cerro de la Neblina, 1700-1800 m, *Maguire et al. 37228*. **COLOMBIA: Norte de Santander:** Sarare region, El Indio, along a branch of the Río Cubugón, 420-480 m, *Cuatrecasas 13064*. **Santander:** Valley of Quebrada Chima in the mountains W of Chima, 7700 ft, *Fassett 25549*. **Cundinamarca:** Caraucha Range, E of Ibama, 13 km E of Yacopí, 2200 m, *Grant 9183*. **Meta:** Río Manzanares Valley, 30 km W of La Esperanza and 52 km W of Villavicencio, 1200 m, *Grant 10106*. **Vaupés:** Río Piraparaná (tributary of the Río Apaporis), *Schultes & Cabrera 17560*. **Caquetá:** Sucre, *Juzepczuk 6514*. **Amazonas:** Near the mouth of the Río Popeyacá (tributary of the Río Apaporis between the Río Piraparaná and Raudal Yayacopi), ca. 700 ft, *Schultes & Cabrera 16182*. **Huila:** Mosquera, 8900 ft, *Little 7715*. **Chocó:** Between Palestina and Agua Negra, Río S. Juan, 5 m, *Cuatrecasas 21555*. **El Valle:** La Cumbre, 1700-2200 m, *Killip 11318*. **Nariño:** S end of Gorgona Island, ca. 0 m, *Killip & García 33106*. **ECUADOR: Esmeraldas:** Parroquia de Concepción, El Sajado on the Río Santiago, 70 m, *Mexia 8449*. **Pichincha:** Quito-Sto. Domingo Road, ca. 1200 m, *Haught 3219*. **Napo-Pastaza:** Between Baños and Mera, 400-500 m, *Mexia 6966*. **Santiago-Zamora:** Valley of the Río Negro and Río Chupianza, on the trail from Sevilla de Oro to Mendez, between Hda. Chontal and Sta. Elena, 3400-4600 ft, *Camp E-809*. **PERU: San Martín:** Top of ridge E of Tingo María, 1020 m, *Allard 21476, 21489*. **Loreto:** Sierra del Pongo, 800 m, *Mexia 6287*. **Huánuco:** Tingo María, 700 m, *Tryon & Tryon 5331*. **Junín:** E of Quimirí Bridge near La Merced, 800-1300 m, *Killip & Smith 23886*. **Cuzco:** Valley of Cosñipata between Yanamayo and Sta. Isabel, ca. 1500 m, *Scolnik 863*. **BOLIVIA: La Paz:** S. Antonio, near Mapiri, 850 m, *Buchtien 1097*. **BRAZIL: Amazonas:** Track from Km. 63, Manaus-Itacoatiara road, *Prance et al. 9079*. **Roraima:** Vicinity of Auaris, 760-800 m, *Prance et al. 9594*. **Minas Gerais:** S. João, *Lindman A181*. **Rio de Janeiro:** Monte do Cochrane, 20-300 m. *L. B. Smith 1348*. **São**

Paulo: Morro Jaraguá, 1000 m, *A. C. Brade 6590*. **Paraná:** Serro do Embeque, 1200 m, *Hatschbach 24951*. **Sta. Catarina:** Morro do Baú, Itajaí, 700 m, *Reitz 3017*. **FRENCH GUIANA:** May 1831, *Leprieur*. **SURINAM;** Brownsberg, 400 m, *Gonggerijp & Stahel 320*. **GUYANA:** Trail from Kaieteur Falls to Tukeit, Potaro River Gorge, *Maguire & Fanshawe 23480*.

LIBERIA: Vicinity of Mt. Coffee, ca. 40 mi inland from Monrovia, 50-150 m, *Cook 122*. **MAURITIUS:** *Pike* in 1867. **MADAGASCAR:** Mont Papanga, 1600-1700 m, *Humbert 6944*.

~ 4. Cochlidium minus (Jenm.) Maxon, Sci. Surv. Porto Rico and Virgin Is. 6: 407. 1926.

Monogramma minor Jenm. Bull. Bot. Dept., n. ser. **4:** 212. 1897. TYPE: Murray's Flat, above Mt. Moses, St. Andrew Parish, Jamaica, *Jenman s.n.* in 1876. (NY!; isotype US!).

RANGE AND HABITAT: Jamaica and Cuba. Proctor (1953) describes this species as epipetric. One Cuban specimen is cited as "Epiphytic or terrestrial in dense clumps." Elevations on two sheets from Cuba are 1350 and 1400 m.

Of *C. minus* from Jamaica, I have seen only the type material. Evidently rare and local, this is also the smallest known species of the genus. Both Maxon (1926) and Christensen (1929) included here a number of specimens from Cuba and Puerto Rico that to me clearly belong to two other species, both undescribed.

SPECIMENS EXAMINED:

CUBA: Oriente: Palma Mocha, 1400 m, *Ekman 5211*. Crest of Sierra Maestra between Pico Turquino and La Bayamesa, 1350 m, *Morton & Acuña 3563*. S side of the crest of the Sierra Maestra W of Aserradero S. Antonio de las Cumbres, region of La Bayamesa, 1400-1500 m, *Morton 9591*.

~ 5. Cochlidium repandum L. E. Bishop, sp. nov.

Filix parvula quae in saxibus arboribusque colonialiter crescens invenitur. Rhizoma ascendens, frondes approximatas et paleas 2-4 mm longas apicibus acuminatis ad basin cordatam per 8-12 cellulas latas ostendens. Stipites tenues atrobrunnei teretes 1-15 mm longi atque diametro 0.2-0.3 mm. Lamina 2-6 cm × 1.0-2.5 mm, chartacea vel subcoriacea, patula vel suberecta, ad apicem rotundata, basin versus acuminata, costa dorsaliter parum prominula vagina sclerotica eius plus minusve hic evidenti at ventraliter costa praecipue per longitudinem fertilem prominenti edenti venulas visibiles quae in hydathodos claras terminant, margine repando aut interdum subintegro, pilis 2-4 cellularibus in margine costaeque faciebus ambabus instructa, stomatibus abaxialibus 55-67 × 47-53 μm, sorifera per partem usque tertiam distalem hic limbo laminali plano aut circum soros conduplicato. Venae steriles simplices, illae fertiles basaliter receptaculares emittentes furcam itidem fertilem quae in venam proximam distalem jungit, hoc modo coenosorum efficientem. Coenosorus in laminam impressus, aliquando aliquantum interruptus. Sporangiorum capsulae subglobosae 100-120 × 95-110 μm, cellulae annuli 10-12, sporae 22-25 μm diametro.

HOLOTYPE: On tree fern bases, Arroyo del Medio, above the falls, Sierra de Nipe, Oriente, Cuba, 450-550 m, *Shafer 3473* (US).

PARATYPES: The following collections from Cuba at US are referable here: *Clément 4631, 4978, 6724, Acuña 12348, Pollard et al. 240, Shafer, 3475, 4110, 8072, 8159*.

RANGE AND HABITAT: Apparently confined to the eastern end of Cuba, Pcia. Oriente, from Sierra de Nipe to Baracoa. Judging from the number of collections, it must be at least locally common at middle altitudes. It is recorded growing on both trees and rocks.

Confounded by Christensen and Maxon with *C. minus and C. jungens*, this species is easily separated by the repand margin and other characters mentioned in the key. *Cochlidium minus* occurs in Cuba only in the Sierra Maestra, where *C. repandum* is absent. Apparently the two species grow at different elevations as well.

6. Cochlidium jungens L. E. Bishop, sp. nov.

Epiphytum parvum in sylvis muscosis vigens. Rhizoma ascendens vel erectum nonnunquam ramosum ac caespitosum, frondibus stipitibusque confertis onustum, paleis 1.5-3 mm longis e basi truncata aut subcordata 8-12 cellulas lata usque ad apicem filiformem acuminate angustatis praeterea instructum. Stipites obsoleti vel usque 10 mm longi alati atrobrunnei 0.2-0.4 mm diametro. Lamina 2-8 cm × 1.5-3 mm, chartacea vel subcoriacea, vulgo erecta, ad apicem rotundata basin versus acuminata, costa utrinque prominula sed vagina atrofusca rarenter evidenti, in margine integro costaque utrinsecus pilis ex 2-8 cellulis constantibus illis interdum raris vel sub aetate provecta carentibus, stomatibus dorsalibus 65-82 × 52-62 μm, sorifera ad apicem vel frondis medio tenus, hac lamina fertili expansa aut super sporangias conduplicata. Venae steriles plerumque simplices, illae fertiles saepe furcatae, receptaculares ad basem venae furcataeque acroscopicae, increbre furca receptaculari adjecta ad venam proximam jungenti et coenosorum facienti. Sporangia capsulis 150-180 × 150-170 μm, cellulis annuli 8-11, sporisque papillosis 26-31 μm diametro.

HOLOTYPE: Epiphytic in mossy forest, top of Morne Micotrin, St. George Parish, Dominica, 3800 ft, *Nicolson 1975* (US).

PARATYPES: The following are also at US: Dominica: *Webster 13376;* Puerto Rico: *Britton 7917, Hess 313, Hioram 335, Shafer 2245, 3647.*

RANGE AND HABITAT: Dominica and Puerto Rico. Epiphyte in cloud forest, 800-1500 m elevation.

This is yet another species formerly confounded with *C. minus*. Actually, with its larger, erect and often crowded fronds, it is hardly even superficially like that species, and finer characters clearly separate the two. Nor does *C. jungens* show any more than a casual resemblnce to *C. repandum* of Cuba.

Of interest in this species is the variation with respect to fusion of the sori. In some plants coenosoral development is complete. But in most the sori are separate, or else show various degrees of soral coalescence. Since some workers have felt the coenosorus to be critical in the generic delimitation of *Cochlidium*, I have chosen the epithet to emphasize that with respect to this character, the species with polypodioid sori are joined to those with coenosori by this species. However, this should not be taken to indicate that *C. jungens* is phylogenetically intermediate between the groups.

7. Cochlidium seminudum (Willd.) Maxon, Sci. Surv. Porto Rico and Virgin Is. 6: 407. 1926.

Blechnum seminudum Willd. Phytogr. 13, *t. 8, f. 2.* 1794. TYPE: Martinique, *Isert s.n.* in 1787 (B not seen; studied from microfiche no. 19587 of Herb. Willd.)

Grammitis seminuda (Willd.) Willd. Sp. Pl. **5:** 140. 1810.

Taenitis graminifolia Hooker, Exotic Fl. **1:** *t. 77.* 1823. TYPE: St. Vincent, *Guilding s.n.* (K not seen).

Taenitis pumila Kaulf. Enum. Fil. 132. 1824, *nom. nov. et superfl.* TYPE: Based on *Blechnum seminudum* Willd.

Taenitis linearis Kaulf. Enum. Fil. 131. 1824. TYPE: Guadeloupe, without collector (Herb. Sprengel, presumably destroyed).

Micropteris blechnoides Desv. Mém. Soc. Linn. Paris **6:** 217. 1827, *nom. nov. et superfl.* TYPE: Based on *Blechnum seminudum* Willd.

Grammitis isertii Swartz, Adnotat. Bot. 65. 1829, *nom. nov. et superfl.*, as "*iserti.*" TYPE: Based on *Blechnum seminudum* Willd.

Pleurogramme graminifolia (Hooker) Presl, Tent. Pterid. 223. 1836.

Pleurogramme linearis (Kaulf.) Presl, Tent. Pterid. 223, *t. 10, f. 2.* 1836.

Pleurogramme pumila (Kaulf.) Presl. Tent. Pterid. 223. 1836.

Monogramma graminifolia (Hooker) Hooker, Sp. Fil. **5:** 124. 1864, as "*Monogramme.*"

Taenitis seminuda (Willd.) Kuhn, Fil. Afr. 59. 1868.

Pleurogramme seminuda (Willd.) J. Smith, Hist. Fil. 178. 1875.

Pleurogramme nuda Goebel, Flora **117:** 119. 1924.

RANGE AND HABITAT: Jamaica, Hispaniola, Puerto Rico, Lesser Antilles, Trinidad, and Venezuela. Christensen (1929) also cites specimens from French Guiana. Due to the usual confusion about Isert's specimens, nineteenth century authors also assigned the species to Africa, where it does not exist.

Cochlidium seminudum is a fairly common, widespread, and larger member of the genus. As as result, it has had an appropriately checkered taxonomic history.

Hooker described *Taenitis graminifolia* without reference to Willdenow's species, suggesting only that it might be identical with *Grammitis graminoides* (=*Cochlidium*) of Jamaica. Although I have not seen type material, the illustration is good and no species is known from St. Vincent superficially similar to *C. seminudum*.

Willdenow's type is a small plant of this species. Kaulfuss assigned the name *Taenitis pumila* to this specimen and differentiated his *Taenitis linearis* as being twice as large and stipitate. The type was undoubtedly destroyed along with the rest of the ferns of Sprengel's herbarium, so that the application of the name can never be certain. However, assuming that it represents an otherwise known taxon, one part of Kaulfuss' description, "Frons . . . hinc [e medio] angustata in caudam elongatam producta," could only apply to this species.

Presl erected his genus *Pleurogramme* to include both of Kaulfuss' species as well as Hooker's *T. graminifolia*. Therefore, all three names in Presl's genus are reducible to a single species concept.

As pointed out by Christensen, Goebel (1924) sought to clear the confusion of this species with *C. punctatum*. The Brazilian plants frequently had been included in the same species concept as the Caribbean *C. seminudum* by nineteenth century workers, but Goebel clearly established the two populations as distinct. Unfortunately, he applied the name *Pleurogramme seminuda* to the Brazilian species and gave the new name *Pleurogramme nuda* to the Caribbean population. No type was cited, but the intended application of the name is obvious.

The most distinctive characteristic of this species is the constriction of the lamina through the fertile portion. No other species exhibits this feature. The sori are impressed into the dorsal surface, but the limb of the fertile lamina is usually

flat. Only rarely is it conduplicately folded around the sporangia. In such cases, the fertile portion is generally falcate as well.

REPRESENTATIVE SPECIMENS EXAMINED:

JAMAICA: Portland: E slope of the John Crow Mountains 1.5-2.5 mi SE of Ecclesdown, 1500-2500 ft, *Proctor 10491*. **HISPANIOLA: Samaná:** Top of Pan de Azucar, ca. 510 m, *Ekman H14883*. **PUERTO RICO:** El Yunque, Serra de Luquillo, 2500-3000 ft, *Chase 6730c*. Loma Icaco, Sierra de Naguabo, 210-675 m, *Shafer 3457*. **ST. KITTS:** Molyneux Estate, *Britton & Cowell 684*. **NEVIS:** Nevis Peak, summit and adjacent ridge, 900-1095 m, *A. C. Smith 10559*. **MONTSERRAT:** Upper W spur of Chance's Mountain, 2000-3000 ft, *Proctor 19102*. **GUADELOUPE:** Bains Jaunes, 600 m, *Questel 2003*. **DOMINICA:** Vicinity of Fresh Water Lake near Laudat, 450-600 m, *A. C. Smith 10303*. **MARTINIQUE:** Deux Choux, 460 m, *Stehlé 3423*. **ST. VINCENT:** Soufrière, 2000 ft, *Eggers 6857*. **GRENADA:** *Sherring 96*. **TRINIDAD:** *Bot. Gard. Herb. 1259*.

VENEZUELA: Nueva Esparta: San Juan Mountain, Island of Margarita, 600 m, *Johnston 186*. **Sucre:** NE of Güiria, N of Puerto de Hierro, Cerro Patao, Peninsula de Paria, 800-825 m, *Steyermark & Agostini 91125*.

8. Cochlidium punctatum (Raddi) L. E. Bishop, comb. nov.

~*Grammitis punctata* Raddi, Pl. Bras. **1:** 11, *t. 22, f. 1*. 1825. TYPE: Brazil, *Raddi s.n.* (presumably PISA not seen).

Polypodium ? punctatum (Raddi) Hooker, Sp. Fil. **4:** 172. 1862.

Grammitis paucinervata Fée, Crypt. Vasc. Brés. **2:** 51, *t. 96, f. 1*. 1873. TYPE: Pico da Tijuca, Est. Rio de Janeiro, Brazil, *Glaziou 5384* (presumably RB not seen; isotypes B, C-*fide* C. Chr., NY!).

Monogramma rudolfii Rosenst. Festschr. Alb. v. Bamberg 63. 1905. SYNTYPES: Tresbarras-serra, Est. Sta. Catharina, Brazil, 900 m, *Schmalz 162* (S; isosyntype NY!); Rio Grande, Est. São Paulo, Brazil, *Wacket 45* (S; isosyntype NY!).

Polypodium paucinervatum (Fée) C. Chr. Ind. Fil. 332. 1905.

Cochlidium paucinervatum (Fée) C. Chr. Dansk Bot. Ark. **6**(3): 22. 1929.

RANGE AND HABITAT: Southeastern Brazil, known from the states of Minas Gerais, Rio de Janeiro, São Paulo, Paraná, and Sta. Catarina. Epiphytic or occasionally epipetric, at 400-1300 m elevation.

It is unfortunate that Christensen (1929) adopted Fée's epithet for this species, even though admitting the probable identity of Raddi's earlier species. He states, "As to some points Raddi's description and figure do not agree perfectly with *C. paucinervatum*, and I therefore prefer not to use Raddi's specific name although it is fully available and although I believe that his species is identical with *Gr. paucinervata*." Although I sympathize with Christensen's reluctance to adopt a species whose type he had not seen, in this case I believe it to be justified and necessary.

Raddi's plate is quite good. It shows well the general habit of this species. The only abnormality exhibited, and the one which no doubt disturbed Christensen, is that one of the three fertile fronds is shown with a discontinuous coenosorus. But this is not uncommon in species of the genus with coenosori, and the other two fronds show continuous soriation. Another point concerning the drawing is that the fronds in ventral view show conspicuous hydathodes; indeed, these are celebrated in Raddi's name. These dark, very evident hydathodes constitute a conspicuous feature of many, but not all, specimens of this Brazilian species.

Geographical evidence for the identity of Raddi's species may also be cited. No other remotely similar species is known to occur in southeastern Brazil, but the present one must be fairly common. Raddi did much of his collecting in the area of

Rio de Janeiro, well within the species' range. It seems most unlikely that he gathered a very similar species collected by no subsequent worker but failed to notice the one in question.

In contrast to Raddi's drawing, that of Fée is almost unidentifiable. Even the Glaziou collection on which it is based is so depauperate that attention to microcharacters and a consideration of range are necessary to make a reasonable assignment to species. Interestingly enough in the light of the above discussion, the NY plant has round sori that appear superficially polypodioid, and Fée's species was so described. This condition, though, seems best explained by considering the material subfertile.

Monogramme rudolfii Rosenst. was based on two syntypes. Duplicates of each at NY belong clearly to the present species concept. But since I have not seen the original material and since the selection seems not immediately necessary for nomenclatural purposes, I decline to designate a lectotype.

Goebel (1924) presented a detailed comparison of this species with the Caribbean *C. seminudum*. To his distinctions I would add that the rhizome scales of *C. punctatum* are generally 20-30 cells wide at the base, whereas those of *C. seminudum* are half as many cells wide. The lamina of the latter species is abruptly contracted through its fertile length, whereas that of the former is of uniform width. The sporangial capsules of the Brazilian plant are somewhat obpyriform and 200-250 μm long; those of *C. seminudum* globose and 100-150 μm long.

As Goebel pointed out, the fertile veins generally do not quite fuse in this species. This provides yet another example of imperfect coenosoral development. However, this discontinuity is usually discernible only in cleared specimens and is scarcely detectable externally.

REPRESENTATIVE SPECIMENS EXAMINED:

BRAZIL: Minas Gerais: Bello Horizonte, Serra do Piedade, 1300 m, *Foster & Foster 556*. **Rio de Janeiro:** Itatiáia National Park, S face of Mt. Itatiáia, *Eiten & Eiten 7524-C*. **São Paulo:** Rio Grande, Aug 1913, *A. C. Brade*. **Paraná:** Serra do Capivary Grande, *Hatschbach 8235*. **Sta. Catarina:** Tresbarraserra, 1000 m, *Schmalz (Ros. Fil. Austrobras. Exs. 73)*.

9. Cochlidium linearifolium (Desv.) Maxon ex C. Chr. Dansk Bot. Ark. 6(3): 23. 1929.

Monogramma linearifolia Desv. Ges. Naturf. Freunde Berlin Mag. **5:** 302. 1811. TYPE: French Guiana, without collector (P not seen).

Grammitis linearifolia (Desv.) Steudel, Nomencl. Bot. **2:** 187. 1824.

Pleurogramme immersa Fée, Mém. Foug. **3:** 37. 1852, *nom. nov. et superfl.* TYPE: Based on *Monogramma linearifolia* Desv.

Pleurogramme linearifolia (Desv.) Moore, Ind. Fil. xxvii. 1857.

Monogramma immersa (Fée) Hooker, Sp. Fil. **5:** 125. 1864, as "*Monogramme*."

RANGE AND HABITAT: I have seen specimens from Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Guyana, and Brazil. Christensen (1929) reports it from Tovar, Venezuela. Although this species is to be expected in Venezuela, I suspect any specimen from the elevation of Tovar would likely be *C. rostratum*. I have seen no material from the Caribbean, where Christensen reports specimens from Cuba, Haiti, and Guadeloupe. The Ekman

collection from Haiti is definitely *C. rostratum*, and the others need re-examination. *Cochlidium linearifolium* is an epiphytic species of the lowlands, attaining a maximum elevation of 800 m.

Neither Christensen nor I have seen Desvaux's type. However, because of the preference of *C. rostratum* for high elevations, I think it unlikely that the specimen represents that species. Another possibility is that of confusion with *C. seminudum*, which is reported from French Guiana. There is nothing in Desvaux's description to indicate difference from this species, except the note that the fronds are subfalcate. This is very rarely the case in *C. seminudum*, whereas falcate fronds are common in *C. linearifolium*.

This species has been difficult to distinguish from *C. rostratum*. By recognizing the altitude difference, it has been possible to correlate the prominent hydathodes with smaller sporangial measurements, and therefore to give a better circumscription of the concept than did Christensen, whose venation characters do not hold in my preparations. But the situation is not so clear-cut as would be liked. For instance, the two Costa Rican specimens I have assigned here are really intermediate, both in characters and elevation.

The capsules of specimens included here are often little more than half the size of those of *C. rostratum*, and the stomata generally are smaller as well. This suggests a difference in chromosome number between the two species. I suspect that cytological investigation might show more biosystematic complexity in this area of the genus than can be detailed from herbarium material alone.

REPRESENTATIVE SPECIMENS EXAMINED:

GUATEMALA: Alta Verapaz: Cubilquitz, 350 m, *von Tuerckheim 8372*. **BELIZE:** Mountain Pine Ridge, *Bartlett 11762*. **HONDURAS: Cortés:** E shore of Lake Yojoa, 360 m, *Williams & Molina 11441*. **NICARAGUA:** SE of La Tronquera, 50 m, *Molina 15003*. **COSTA RICA: Puntarenas:** Osa Peninsula on ridge 9.5 km W of Rincón de Osa, 600 m, *Lellinger 676*. **San José:** S. Isidro del General, 2500 ft, *Stork 3106*. **PANAMA: Panama:** Cerro Jefe, 10 mi S from Goofy Lake in Cerro Azul, *Correa & Dressler 171-B*. **Darién:** Summit of Cana, 2500 ft, *Stern et al. 533*.

COLOMBIA: Amazonas–Vaupés: Jinogojé, Río Apaporis, *Schultes & Cabrera 16742*. **Chocó:** Corcovada Region, upper Río San Juan, 200-275 m, *Killip 35341*. **Valle:** Buenaventura, 0-10 m, *Killip 11723*. **BRAZIL: Amapá:** Rio Iaue 0.5 km E of confluence with the Rio Oiapoque, *Irwin et al. 47926*. **Pará:** Vicinity of Cachoeira, Km. 96 of Road BR 22, Capanema to Maranhão, *Prance & Pennington 1705*. **FRENCH GUIANA:** May 1838, *Leprieur*. **GUYANA:** *Ex herb. Jenman*.

— 10. Cochlidium rostratum (Hooker) Maxon ex C. Chr. Dansk Bot. Ark. 6(3): 23. 1929.

Monogramma rostrata Hooker, Sp. Fil. **5:** 122. 1864, as "*Monogramme*." TYPE: Omotepee, Nicaragua, *Wright s.n.* (K not seen; isotype US!). Hooker cites the location as "Island on the Lake Omotepec." Omotepee (now usually spelled Ometepe) is an island in Lago de Nicaragua.

?Pleurogramme gyroflexa Christ in Pittier, Prim. Fl. Costar. **3**(1): 10. 1901. TYPE: Valley of the Río General, Pcia. S. José, Costa Rica, 700 m, *Pittier 12061* (BR or P not seen).

?Monogramma gyroflexa (Christ) C. Chr. Ind. Fil. 430. 1906.

Cochlidium rostratum var. *areolatum* C. Chr. Dansk Bot. Ark. **6(3):** 25. 1929. TYPE, Morne Colombeau, Anse-à-Foleur, Haiti, *Ekman H-4376* (BM not seen; isotype US!).

RANGE AND HABITAT: Cuba, Jamaica, Hispaniola, Guadeloupe, Mexico (Oaxaca), Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, Panama, Venezuela, and Colombia. Epiphytic, at 700–2600 m elevation.

The type represents an extreme form. The sterile lamina is narrow and erect, the fertile strongly conduplicate, falcate, and with a long, sterile apex or "rostrum." I agree with Christensen (1929) that there seem to be all intermediates between this and the forms with wider, laxer, and flat leaves. He took plants of the latter sort to be representative of *Pleurogramme gyroflexa* Christ, although he did not indicate that he had seen the type. This type needs checking; the elevation given in the original description is low for *C. rostratum*, and most workers have not distinguished this species well from *C. linearifolium*.

Christensen removed all Caribbean material to his variety *areolatum*, which was characterized solely by the usually anastomosing veins. The venation is visible only in cleared specimens, and I have found such areolation to be rather casual in my preparations. Since these plants are not otherwise different from those of continental populations, I believe a variety based on such a weak, occult character to be trivial.

The single Mexican specimen that I have seen (*Mickel 914*) needs special mention. The hydathodes are quite conspicuous, as in *C. linearifolium*. In addition the sporangia are a bit small for *C. rostratum* (240–270 μm). However, I retain it here on the basis of the large spores (50–55 μm) and the elevation (ca. 7000 ft.). Certainly the population merits closer study.

REPRESENTATIVE SPECIMENS EXAMINED:

CUBA: Oriente: Crest of the Sierra Maestra between Pico Turquino and La Bayamesa, 1350 m, *Morton & Acuña 3549*. **JAMAICA: Portland:** John Crow Peak, 6000 ft, *Fawcett*. **HAITI:** Marmelade, Morne Belle-Terre, Massif du Nord, ca. 1100 m, *Ekman H8211*. **GUADELOUPE:** Bains Jaunes, 950 m, *Stehlé 341*, 800 m, *Stehlé 1096*.

MEXICO: Oaxaca: Valley of the Yelagago River ca. 20 mi NE of Villa Alta, 6800-7200 ft, *Mickel 914*. **GUATEMALA: Alta Verapaz:** Senahu, Cerro Sillab, *Hatch & Wilson 164*. **HONDURAS: Francisco Morazán:** Rancho Quemado, above S. Juancito, 2100 m, *L. O. Williams 18518*. **EL SALVADOR: Santa Ana:** El Trifinio, Cordillera Miramundo, 2000-2200 m, *Molina, Burger & Wallenta 16796*. **COSTA RICA: Alajuela:** Vicinity of Fraijanes, 1500-1700 m, *Standley & Torres 47486*. **Heredia:** Vara Blanca de Sarapiquí, 1750 m, *Skutch 3322*. **San José:** Las Nubes, 1500-1900 m, *Scamman 7260*. **Cartago:** Near La Sierra, ca. 25 km S of Cartago, 2000 m, *L. O. Williams et al. 28060*. **PANAMA: Chiriquí**: Between Alto de las Palmas and the top of Cerro de la Horqueta, 2100-2268 m, *Maxon 5514*.

VENEZUELA: Lara: Fila de Terepaima between Alto de Chuparral and la Loma Redonda, 21-23 km S of Cabudare, 1300-1460 m, *Steyermark et al. 103382*. **COLOMBIA: Meta:** Renjifo Massif, Cordillera La Macarena, 1300-1900 m, *Idrobo & Schultes 974*.

11. Cochlidium proctorii (Copel.) L. E. Bishop, comb. nov.

Grammitis proctorii Copel. Philipp. J. Sci. **80:** 121. 1952, as "*proctori.*" TYPE: East slope of John Crow Mountains, ca. 2 mi SW of Ecclesdown, Jamaica, 2000 ft, *Proctor 5642* (MICH not seen; isotypes IJ-*fide* Proctor 1953. US!).

RANGE AND HABITAT: Known only from the type locality. Epiphytic.

This is the only species of the genus outside South America with sori borne distally on the veins. Among this group of primarily Venezuelan species, it shares with *C. tepuiense* two regular rows of sori which are more or less separate at maturity. Like *C. attenuatum* it has a lightly repand margin, and the thinner texture and dorsally black midrib are similar to *C. furcatum*. *Cochlidium proctorii* has more abundant marginal hairs than other species of the genus. In *C. jungens* there are occasionally fairly numerous hairs, but this species is easily separable

from *C. proctorii* by its erect habit, thicker texture, green midrib, entire margin, and larger sporangial capsules (length 150–180 vs. 100–140 μm).

12. Cochlidium furcatum (Hook & Grev.) C. Chr. Dansk Bot. Ark. 6(3): 20. 1929.

Grammitis furcata Hook. & Grev. Ic. Fil. *t. 62.* 1828. TYPE: Guyana, *Parker s.n.* (K not seen).

?Mecosorus nudus Klotzsch, Linnaea **20:** 405. 1847. SYNTYPES: Guyana, *Rich. Schomburgk 1187, 1851* (B neither seen).

Polypodium furcatum (Hook. & Grev.) Mett. Abh. Senckenberg Naturf. Gesell. **2:** 34. 1856, *non* Swartz, 1801 *nec* Desv., 1827 *nec* Roxb., 1844.

Polypodium dicranophyllum C. Chr. Ind. Fil. 331. 1905, *nom. nov.* TYPE: Based on *Grammitis furcata* Hook. & Grev.

Grammitis dicranophylla (C. Chr.) Vareschi, Fl. Venez. **1:** 874. 1969, *nom. illeg.*

RANGE AND HABITAT: Guyana, Trinidad, Venezuela, Colombia, Brazil. Epiphyte at 600–2000 m elevation. Reports from Jamaica exist, but I have seen no specimens, Proctor (1953) does not mention it, and I doubt that it occurs there.

This and the following four species constitute a group whose taxonomic disposition is still unsatisfactory. The taxa remain refractory in spite of considerable effort to delimit the species on the basis of microscopic characters. I believe that hybridization is occuring here. This, coupled with the reduction of already small plants in exposed habitats, has resulted in a number of collections which I am unable to place with assurance. My treatment here is tentative and one which does least violence to existing species concepts and nomenclature.

Cochlidium furcatum and *C. tepuiense* are the two commonest, most distinctive, and most stable entities, although even they seem to intergrade with one another and each with other species. *Cochlidium attenuatum* and *C. connellii* exist as identifiable concepts, but are less discrete and more variable. I accept them as species partially because both names are available in the genus. *Cochlidium wurdackii* is a rare but distinct entity worthy of specific recognition. I feel strongly that only careful field observation, perhaps in conjunction with cytological data, will resolve the biosystematic problems with these species.

Although I have not seen the type of the present species, the specimen is fairly well illustrated and is from Guyana, where the species is widespread. In addition, this is the species most regularly having dichotomous fronds. Therefore, I believe the name to be properly applied.

Mecosorus nudus Klotzsch is more problematic. Copeland (1952) with good reason referred the name to *C. furcatum*, but neither of us have seen the type and the original description is hardly definitive. Schomburgk did collect from Mt. Roraima where *C. attenuatum* and *C. connellii* occur. Since the fronds are described as very rarely bifid, it is possible that the type material represents one of those species. It should be noted that Copeland (1947) suggested this species for the type of *Mecosorus*. The type, of course, must be *Polypodium persicariifolium* Schrad., as this was the type and sole species of the earlier *Microgramma* Presl, which Klotzsch illegitimately adopted as a section of his new genus.

Cochlidium furcatum is the only South American member of the genus with free, distally borne sori which has been found outside the Guyana Highlands. Other workers have emphasized the simple fertile veins and forked fronds to

define this species. Unfortunately, both simple fronds and forked fertile veins occur here, and forked fronds are found occasionally in the other species. Several other features help characterize this concept. The small sporangial capsules, mostly 110-140 μm long, well separate *C. furcatum* from all but *C. tepuiense*, which has capsules mostly 140-170 μm. The present species typically has the sori irregularly disposed and the lamina expanded around the receptacle, resulting in the fertile portion of the frond being irregularly repand. *Cochlidium tepuiense* has entire fronds bearing two regular rows of sori. The lamina of *C. furcatum* is much thinner than that of the following four species, and the dark perivascular sclerenchyma of the midrib is typically visible on the back. This character especially removes the species from *C. connellii*, which has thickly coriaceous fronds. The repand sterile lamina and very narrow fronds distinguish *C. attenuatum* and *C. wurdackii* respectively from *C. furcatum*. I have seen plants apparently intermediate between *C. furcatum* and each of the next three species.

REPRESENTATIVE SPECIMENS EXAMINED:

VENEZUELA: Bolívar: Salto de Iwaracarú-merú, at the W end of Sororopán-tepuí, 1615 m, *Steyermark 60227*. **Amazonas:** Vicinity of Base Camp, Cerro Sipapo (Paráque), *Maguire & Politi 27943*. **COLOMBIA: Cundinamarca:** Las Cascades, S side of Guavio River 18 km NE of Gachalá, 2070 m, *Grant 10517*. **Vaupés:** Río Piraparaná, *Schultes & Cabrera 17069*. **TRINIDAD:** Las Lapas Road, 2000 ft, *Hombersley 277*. **SURINAM:** Hendriktop, 1080 m, *B. W. 5709a*. **GUYANA:** Below Tukeit, Potaro River Gorge, *Maguire & Fanshawe 23484*. **BRAZIL:** *Glaziou 12368*.

13. Cochlidium tepuiense (A. C. Smith) L. E. Bishop, comb. nov.

Polypodium tepuiense A. C. Smith in Gleason & Killip, Brittonia **3:** 148. 1939. TYPE: Mt. Auyán-tepuí, Edo. Bolívar, Venezuela, 1850 m, *Tate 1248* (NY!; isotype US!).

Grammitis tepuiensis (A. C. Smith) Vareschi, Fl. Venez. **1:** 871. 1969.

RANGE AND HABITAT: Widespread in the highlands of SE Venezuela. Epiphytic, at 1000-2000 m elevation.

This is the largest of the Guyana Highlands group of species. It is best characterized by the broad fronds up to 3 mm wide bearing two regular rows of sori which at maturity may be confluent lineally but are separate across the midrib. The entire margin separates it from *C. furcatum* and *C. acuminatum*. The larger size and somewhat separate sori remove it from the present concept of *C. connellii*.

SPECIMENS EXAMINED:

VENEZUELA: Bolívar: Headwaters of the Río Venamo, northern slopes of Cerro La Danta, NW of Cerro Venamo, 1040 m, *Steyermark & Nilsson 53*. Headwaters of the Río Chicanán 80 km SE of El Dorado, Sierra de Lema, 700 m, *Steyermark 89412*. NE portion of Cerro Sarisariñama, Meseta del Jaua, 1400 m, *Steyermark et al. 109184*. **Amazonas:** Cerro Sipapo, *Maguire & Politi 27615-B, 27708, 27744*.

14. Cochlidium attenuatum A. C. Smith in Gleason, Bull. Torrey Bot. Club 58: 308. 1931.

Grammitis tatei Copel. Philipp. J. Sci. **80:** 120. 1952, *nom. nov*. TYPE: Based on *Cochlidium attenuatum* A. C. Smith in Gleason, *non G. attenuata* Kunze.

TYPE: Mt. Duida, Venezuela, 5500-6000 ft, *Tate 428* (NY! isotype US!)

RANGE AND HABITAT: Fairly widespread through the Guyana Highlands of Venezuela and Guyana. Epiphytic or epipetric at 1500-2000 m elevation.

This species is somewhat marginally represented by the type of *C. attenuatum*. The smaller plants of the type collection show very narrow fronds with essentially entire sterile laminae, superficially resembling *C. wurdackii*. However, the specimens have large sporangia, long scales, large stomata, and the larger plants do have repand margins. So I feel that this type is for now sufficiently well placed with, if not especially typical of, this species concept.

I have applied this name to plants whose most conspicuous and distinctive feature is the lightly repand sterile portion of the frond. Such plants agree in other characters as well. The fronds are narrow, often 1 mm or less in width; in large plants up to 15 cm they may reach 2 mm across. The sori are usually confined to the distal quarter of the frond, which is here a bit expanded, and are somewhat irregularly disposed, but more or less confluent at maturity. The sporangial capsules are larger than in the last two species, 160-220 μm long, and the stomata and scales are larger than those of *C. wurdackii* (65-90 × 55-65 μm and 2-3 mm long, respectively, in *C. attenuatum*).

REPRESENTATIVE SPECIMENS EXAMINED:

VENEZUELA: Bolívar: Cerro Guaiquinima, Río Paragua, open savanna 1 km S of Cumbre Camp, 1800 m, *Maguire 32796*. SW portion of Cerro Jaua, 2228-2250 m, *Steyermark et al. 109604*. Mt. Roraima, *im Thurn 166*. Upper cumbre of the NW cumbres of Churi-tepuí (Muru-tepuí), 2250-2300 m, *Wurdack 34242*. Headwaters of the Río Chicanán SW of El Dorado, Serra de Lema, 500 m, *Steyermark 89598*. **Amazonas:** Río Cunucunuma, Cerro Huachamacari, 1800 m, *Maguire et al. 30305*.

15. Cochlidium connellii (C. H. Wright) A. C. Smith, Bull. Torrey Bot. Club 57: 179. 1930.

Polypodium connellii Baker ex C. H. Wright in N.E. Brown, Trans. Linn. Soc. London, Bot. 6: 82. 1901. SYNTYPES: Summit, Mt. Roraima, British Guiana, *McConnel & Quelch 570* (K not seen; isosyntypes NY! US!), *111* (K not seen), *118* (K not seen).

RANGE AND HABITAT: Guyana Highlands of Venezuela and Guyana. Epipetric, terrestrial, or occasionally epiphytic; at 1600-2300 m elevation.

This is manifestly and admittedly the least satisfactory species concept in this treatment of the genus. I have followed general usage and, I hope, the original description by applying the name to those plants with erect, coriaceous, congested fronds growing in tufts at higher elevations. These typically have fronds 3-6 cm long and 1.5-2 mm wide (*Steyermark 59673, Vareschi & Foldats 4777, 4866, 4887*). Except for the size, shape, and habit of the fronds, these are otherwise similar to *C. attenuatum* in their larger sporangial capsules 170-220 μm long, stomata 70-95 μm long, and distal, somewhat irregular sori. Also, the sterile laminae sometimes are very slightly repand. Contracted plants of *C. attenuatum*, such as *Steyermark 109604*, differ only in their narrower, more repand fronds. On the other hand, occasional plants with large sporangia seem very close to reduced examples of *C. furcatum* or *C. tepuiense*. As mentioned earlier, I believe that only field knowledge of these plants can clarify the problems here.

The typification of the name *C. connellii* and the present species concept must remain open to question. The protologue included three different numbers. I have seen duplicates of only one of these, and even the plants included there are not uniform. For instance, the sheet at US has three mounted plants. One has lightly

repand fronds ca. 1 mm wide and does not differ from the concept of *C. attenuatum* as accepted here. The other two have entire, coriaceous fronds ca. 1.5 mm wide and up to 7 cm long with large sporangia. The sori are irregularly distant with the lamina expanded around them, much as in *C. furcatum*. These plants do not fit well into any of the species here recognized. However, until all of the original material can be examined and until a greater understanding of the Guyana Highlands *Cochlidium* species is attained, I think it unwise to disrupt current usage of the *C. connellii*.

REPRESENTATIVE SPECIMENS EXAMINED:

VENEZUELA: Bolívar: Upper part of Auyan-tepuí, 2300 m, *Vareschi & Foldats 4887*. Plateau portion of SE-facing slopes of Ptari-tepuí, 1600 m, *Steyermark 59673*. Cumbre of the east-central portion of the Meseta de Jáua, ca. 60 Km. NW of the misión de Campamento Sanidad on the Río Kanarakuni, 1922-2100 m, *Steyermark 97988*. **Amazonas:** Cerro Sipapo (Paráque), 5500 ft, *Maguire & Politi 27615-A*. SE escarpment of Cerro Huachamacari, Río Cunucunuma, 1900 m, *Maguire et al. 30158*.

16. Cochlidium wurdackii L. E. Bishop, sp. nov.

Filicula gracillima tegetiformis quae ripas alpinas incolit. Rhizoma tenue repens frondes paulo dissitas gerens paleisque minutis triangularibus 0.4-0.7 mm longis ad basin 4-8 cellulas latis exigue vestitum. Stipes 2-10 mm longus basin versus teres 0.2-0.4 mm diametro. Lamina coriacea 3-7 cm × 0.5-1 mm, linearis fili similis, base acuminata apice rotundata aut obtusa, venatione et vagina costae sclerotica vix evidenti, costa e pagina ventraliter conspicue dorsaliter paulum exstans, sub juventute pilis pluribus catenatis ex 4-7 cellulis constantibus in costa utrimque praedita autem alibi et sub maturitate glabra, stomatibus abaxialibus 47-57 × 36-45 μm. Venae steriles plerumque simplices ad costam fere parallelae in hydathodos claras in regione mediali terminantes, illae fertiles ramo sorifero acroscopico distaliter recto neque non ramo breviore basiscopico patenti. Sori distales, pauci 1-5 in quaque fronde fertili, inordinate dispositi, lamina in area sori latitudine expansa. Sporangiorum capsulae 160-190 × 130-170 μm, annuli cellulae 9-11, sporae 28-36 μm diametro.

HOLOTYPE: Abundant in mats on rocks along Río Sarvén, 1 km downstream from Camp 9, Sarvén-tepuí, Edo. Bolívar, Venezuela, 1200 m, *Wurdack 34349* (US).

PARATYPE: Terrestrial, frequent on river banks, along Río Tirica below Upper Falls above summit camp, central section of Chimantá Massif, Edo. Bolívar, Venezuela, 1940 m, *Steyermark & Wurdack 577 (US)*.

This apparently localized species differs from all others of the genus in its very small rhizome scales. Other characters which distinguish it from species with discrete sori include the slender, creeping rhizome, the very narrow fronds, and the smaller stomata. The habitat is also unusual in the genus. Both collections show the plants forming mats in sandy soil. All other species are epiphytic or grow among epipetric bryophytes.

The species is named for John J. Wurdack, not only for his responsibility for both gatherings, but also in recognition of the effect his considerable field effort has had in the advance of our knowledge of neotropical floras.

SPECIES IGNOTA NECNON DUBIA

Pleurogramme myrtillifolia Fée, Mém. Foug. 3: 38. 1852; 5: *t. 10c*. 1852.

Monogramma myrtillifolia (Fée) Hooker, Sp. Fil. **5:** 125. 1864, as "*Monogramme.*"

TYPE: Habitat in monte Tisis [Mexico?], collector unknown (possibly RB not seen).

This species is described as having small, spathulate, very thick leaves scattered on a long-repent rhizome. The locality is quite unknown to me, and it may not be American. Fée's illustrations of the whole plant very much suggest one of the smaller species of *Microgramma* or *Lemmaphyllum*, and the details could conceivably be juvenile or misinterpreted. Despite its inclusion in *Pleurogramme*, I very much doubt that this plant is a *Cochlidium*, but only by the rediscovery of Fée's type can the matter be settled.

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SHORTER NOTES

A DELETION FROM THE PTERIDOPHYTE FLORA OF NEBRASKA.—In the "Atlas of the Flora of the Great Plains" (Great Plains Flora Association, Iowa State University Press, Ames, 1977), *Lycopodium annotinum* was listed for the first time for Nebraska.The report was based on the following specimen: Kennedy, Cherry County, Nebraska, *Rev. John M. Bates s.n.* in 1892 (NEB 167907). Recently I had the opportunity to examine this specimen and found it to be correctly determined. However, debris at the base of the plant indicated that this specimen could not have been collected in Nebraska.

Abundant in the debris were leaves and cone scales, both staminate and pistillate, of *Picea glauca,* which does not occur in Nebraska. In addition, three mosses were discovered: *Polytrichum commune, Rhytidiadelphus triquetrus,* and *Thuidium minutulum*. The latter two species are not known in Nebraska. Considering the ranges of the spruce and mosses, the *Lycopodium* likely came from somewhere in the northeastern United States, where Bates is known to have collected on several occasions. In addition, the handwriting on the specimen's

label is not that of Bates. For these reasons, it is assumed that there was a mixup of one sort or another which caused this error, and, therefore, *Lycopodium annotinum* must be eliminated from the flora of Nebraska and the Great Plains. For making the necessary moss determinations I thank Steve Churchill, Botany Department, University of Kansas.—*Ralph E. Brooks, University of Kansas Herbarium, 2045 Avenue A, Campus West, Lawrence, KS 66044.*

CYSTOPTERIS TENNESSEENSIS IN ALABAMA.—The Tennessee Bladder Fern, *C. tennesseensis* Shaver, has been listed as occurring in northeastern Alabama by Dean (Ferns of Alabama, 1969). It was found at the mouth of Nick-a-Jack Cave in Jackson County, just within the state line. Now two additional localities can be reported from the north-central part of the state.

In August 1975, *C. tennesseensis* was found growing around a sinkhole in Morgan County. This locality is in Newsome Sinks, a large lime-sink valley about 20 miles south of Huntsville. The specimens lack the foliar bulblets usually present on plants of *C. tennesseensis* and were identified initially as *C. fragilis* var. *mackayi* Lawson. However, samples were identified recently as *C. tennesseensis* by Dr. W. H. Wagner, Jr. Vouchers *(Short 386)* are deposited at AUA and MICH, and later collections *(Short 887)* from the same locality will be distributed by AUA.

In the summer of 1976, a fern gametophyte with young sporophyte was found growing in damp soil under shrubs at the residence of Dr. William A. Short of Athens, in Limestone County. The development of this plant was observed, and by June 1977 the sporophyte had produced sori characteristic of *Cystopteris* and bulblets characteristic of *C. tennesseensis*. The habitat was unusual for this species; the fern grew in deep soil containing only a few pieces of limestone gravel from a nearby driveway. A voucher *(Short 905)* is deposited at AUA.

Shaver (Ferns of Tennessee, 1954) suggested that *C. tennesseensis* may have originated from hybridization between *C. bulbifera* (L.) Bernh. and *C. protrusa* (Weath.) Blasdell, since many of its characteristics are intermediate between these species. It reproduces by spores as well as bulblets, and probably is an allopolyploid, according to Blasdell (Mem. Torrey Bot. Club 21(4): 51. 1963).

Cystopteris tennesseensis generally grows on damp, shady, calcareous-rock outcrops. It ranges from northern Alabama to Michigan westward to Kansas, mainly in upland physiographic provinces, according to Wherry (The Fern Guide, 1961). It also has been reported on marl outcrops in the coastal plain of North Carolina, according to Radford, Ahles, and Bell (Manual of the Vascular Flora of the Carolinas, 1968), where we observed it in October 1977. The knowledge of this species' distribution in Alabama is still incomplete, but suitable habitats are frequent in the northern counties and occasionally occur in the coastal plain. It can be inferred that *C. tennesseensis* probably is more widely distributed in Alabama than previously has been believed.—*John W. Short* and *John D. Freeman, Department of Botany and Microbiology, Auburn University Agricultural Experiment Station, Auburn, AL 36830.*

EQUISETUM × LITORALE RECORDED FOR MINNESOTA.—On 8 August 1977, while preparing an inventory of the floodplain flora of parts of the upper Mississippi River and its tributaries, one of us (SDS) collected a specimen of *Equisetum* from a large colony that was growing under a stand of *Salix interior* on dredge spoils and disturbed floodplain at the confluence of Valley Branch Creek and the St. Croix River (Mile 11.75) in Washington County, MN. The specimen was identified by one of us (JHP) as *Equisetum* × *litorale* Kuhl., which is the hybrid between *E. arvense* and *E. fluviatile*. Dr. Richard L. Hauke, of the University of Rhode Island, verified the determination. A voucher *(Swanson 2878)* is deposited at University of Wisconsin-La Crosse (UWL). According to Dr. Gerald B. Ownbey, of the University of Minnesota, this is the first record for Minnesota.—*James H. Peck* and *Steven D. Swanson, Dept. of Biology, University of Wisconsin-La Crosse, La Crosse, WI 54601.*

LYCOPODIUM CERNUUM IN LOUISIANA.—The Nodding Club-moss, recently reported by Eleuterius (Castanea **41:** 180-181. 1976) from Jackson County, Mississippi, has recently been collected in central and southeastern Louisiana.

On 13 Sept 1975, Thomas and an aquatic plants class found several plants along a west-facing bank of the Pearl River Canal east of Louisiana route 41 and Evans Creek in St. Tammany Parish, Sec. 41, T6S, R14E *(Thomas 46276,* NLU). The area was revisited by Thomas and Allen later in the same month, and three populations of *L. cernuum* were observed *(Thomas & Allen 47241,* NLU). No other ferns or fern allies were found. In the spring of 1977, another specimen of *L. cernuum* from St. Tammany Parish was collected by a student at Louisiana State University. Thomas, Landry, and others visited this site in the fall of 1977. The plants were in the bottom of an abandoned gravel pit near Hickory, La. *Lycopodium cernuum, L. appressum,* and *L. carolinianum* all were abundant, along with *Burmannia capitata.*

On 15 Oct 1976, Holmes collected two specimens of *L. cernuum* in a small roadside ditch in a seepage area in a longleaf pine woods along Middle Branch Road in the Red Dirt Game Management Area of Kisatchie National Forest in Natchitoches Parish *(Holmes 2902,* NATC). This area is the largest hillside bog in Louisiana and has an abundance of bog plants, including *Lycopodium appressum, L. carolinianum, Burmannia capitata, Pinguicula pumila,* and *Sarracenia alata.* This area was searched extensively by Holmes and by Thomas on separate occasions in the fall of 1977, but no plants of *L. cernuum* could be located. The winter of 1976 was severe and might have killed these plants, which are at the northernmost and westernmost limit of their range. If this location represents a permanent population, then *L. cernuum* should also be found in Vernon Parish and perhaps in adjoining Texas.—*R. Dale Thomas, Dept. of Biology, Northeast Louisiana University, Monroe, LA 71209; W. C. Holmes, Dept. of Biological Sciences, Northwestern State University of Louisiana, Natchitoches, LA 71457; Charles M. Allen, 111 Lucas Circle, Lafayette, LA 70508; and Garrie Landry, Dept. of Botany, Louisiana State University, Baton Rouge, LA 70803.*

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Trichomanes Gametophytes in Massachusetts

BRUCE McALPIN* and DONALD R. FARRAR**

The final event in the 1976 New England Fern Conference convened by area pteridologists was a morning field trip to Mt. Toby, in Franklin County, Massachusetts. An unexpected find on this foray was the filamentous gametophytes of an unknown species of *Trichomanes*. These were growing far back in crevices in non-calcareous, conglomerate rocks (pH 7) exposed along a small creek at the base of Mt. Toby. This is the habitat typical of the *Trichomanes* and *Vittaria* gametophytes found commonly in the southern Appalachian Mountains (Farrar, 1967, 1971). By shining a flashlight into the dark recesses, plants were seen to be relatively abundant, although individual clones were not extensive. The largest clone occupied an area approximately 50 cm^2, whereas most were less than two cm in diameter. A subsequent foray provided additional specimens from this site.

The discovery of *Trichomanes* gametophytes in Massachusetts is of considerable significance. This site is over 400 miles northeast of the most northerly stations previously known in Hocking County, Ohio and Pendleton County, West Virginia. It is also the first collection of *Trichomanes* from a site well within the area glaciated during the Pleistocene. All previous collections, which extend from West Virginia and Georgia westward to northwest Arkansas, are from unglaciated areas which have existed as dissected uplands at least since the late Tertiary.

Throughout their range in the temperate United States, the gametophytes are sterile. They often lack sex organs and apparently never produce sporophytes. Their reproduction is by vegetative buds, called gemmae *(Fig. 4)*. Sporophytes of two species of *Trichomanes*, *T. boschianum* Sturm ex v. d. Bosch and *T. petersii* A. Gray, occur in the same non-glaciated range as the *Trichomanes* gametophytes. A few diploid populations of *T. boschianum* produce viable spores, but most populations of *T. boschianum* and possibly all populations of *T. petersii* in this area are polyploid and produce aborted spores. Sporophytes of both species produce dispersable vegetative buds.

Although the *Trichomanes* gametophytes in the temperate United States have generally been assumed to be of the same species as these sporophytes, this has not been proven. The occurrence of gametophytes in Massachusetts, over 400 miles from either sporophyte species, decidedly increases the probability that species other than *T. boschianum* and *T. petersii* may be represented. This collection also points out the need for further search in the northeastern United States. It is likely that discovery of *Trichomanes* gametophytes will enlarge the pteridophyte flora of most New England states. We thus encourage field workers in this area to search for these small, alga-like plants *(Figs. 1-4)* and to report to us any additional discoveries. Specimens from Mt. Toby have been sent to the Gray Herbarium, the U. S. National Herbarium, and the Herbarium of the New York Botanical Garden.

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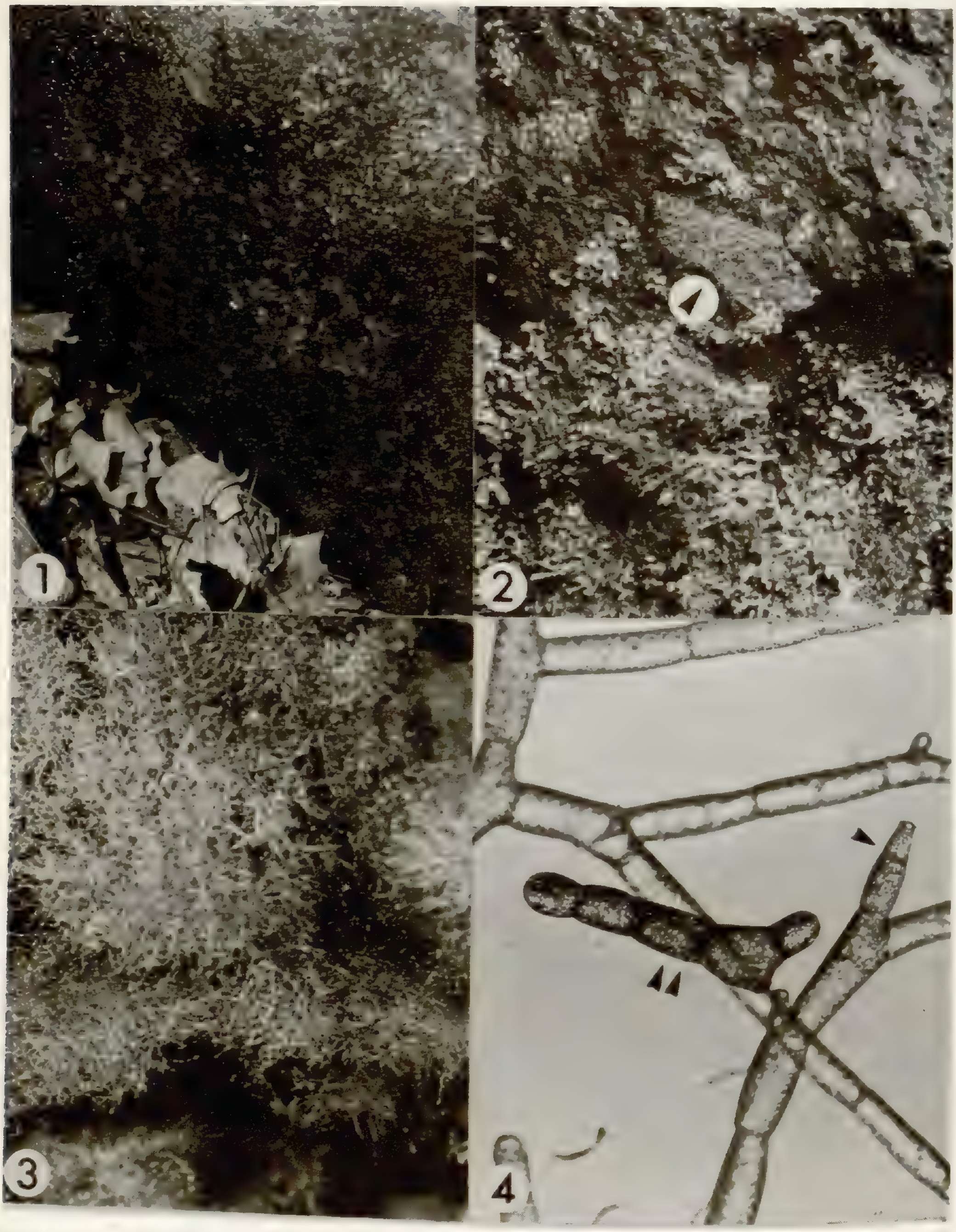

FIGS. 1-4. *Trichomanes* gametophytes. FIG. 1. Dark, overhanging rock outcrop nearly covered by clones of gametophytes, × 1/5. FIG. 2. Clone of gametophytes (arrow) surrounded by various bryophyte species, × ½. FIG. 3. Clone of gametophytes demonstrating growth habit, × 10. FIG. 4. Gametophyte filaments with characteristic gemma (double arrow) and gemmifers (arrow), × 150.

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A New and Unique, Mat-forming Merlin's-grass (Isoëtes) from Georgia

PHILLIP M. RURY*

The quillworts, *Isoëtes* (Lycopsida, Isoëtales), constitute a heterosporous family of about 60 species recognized by botanists since the time of Linnaeus as having fleshy, two-, three- or four-lobed corms with a crown of spirally arranged, ligulate microphylls and numerous dichotomizing roots that emerge in series along the median furrow(s) of the corm.

Vertical stem growth in *Isoëtes* results from a shoot apical meristem that produces sterile and fertile leaves and a central core of primary vascular tissue. Expansion growth is effected by the activity of a lateral meristem or "cambium" that encloses the primary vascular cylinder. During growth in girth, the original corm structure is maintained by radial displacement and seasonal loss of the outer, older leaves, roots, and corm tissue.

Sexual reproduction involves the formation of micro- and megasporangia, the spores of which develop endosporically into male and female gametophytes. Water-mediated cross fertilization produces daughter sporophytes.

Developmentally, young sporophytes exhibit a distinct change in their overall morphology (Paolillo, 1963). During the first 10-15 plastochrons, leaves are produced alternately on either side of the embryonic shoot apex. During this stage, the apical meristem produces neither cauline vascular tissue nor primary stem growth; thus the vasculature of these distichous juveniles consists of a sympodium of traces to leaves and roots on either side of the shoot apex and median furrow. The resultant two-ranked leaf arrangement is lost, however, as soon as the apical meristem becomes large enough to initiate leaf primordia in a spiral sequence. Apparently, this apical enlargement also is responsible for the differentiation of the vascular core and the concomitant inception of vertical stem growth.

Vegetative propagation is rare in *Isoëtes*. Goebel (1879) reported it in *I. echinospora* Dur. Goebel (1905, p. 431) also reported adventitious plantlets on *I. lacustris* leaves in a sporangial or sub-sporangial position in sterile specimens from the Vosges Mountains of France. Similar sterile but viviparous plants of *I. lacustris* were reported from Windmere, England by Manton (1950, p. 255). The developmental origin of such epiphyllous plantlets is not understood and is in need of investigation.

Branching in the upper portions of *Isoëtes* axes, another mechanism of vegetative reproduction, also has been reported (Motelay & Vendryes, 1882; Solms-Laubach, 1902; Eames, 1936, p. 51), and a recent developmental study has revealed basal branching in two species of *Isoëtes* (Karfalt & Eggert, 1977).

With the exception of branching and bud-formation, the quillworts traditionally have been considered as a morphologically uniform family of pteridophytes. The discovery of the Peruvian genus *Stylites* (Amstutz, 1957), however, has expanded

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our biological and morphological concept of the Isoëtaceae. Detailed developmental and morphological studies of *Isoëtes* (e.g. Paolillo, 1963), *Stylites* (Rauh & Falk, 1959 a, b), and the structural intermediate of these two genera, *I. triquetra* A. Br. (Kubitzki & Borchert, 1964), have indicated that the family Isoëtaceae actually represents a polymorphic, clinal complex probably best treated as a single genus.

The profound influence of microhabitat upon *Isoëtes* morphology (Kubitzki & Borchert, 1964; Matthews & Murdy, 1969) must be considered in order to understand the complex polymorphism encountered within this family. The recent recognition of the following new and unique species of *Isoëtes* that is a narrow endemic in the Piedmont of Georgia further emphasizes the influence of habitat upon *Isoëtes* morphology and supports the concept of the extant Isoëtaceae as a polymorphic, monogeneric family of pteridophytes.

FIG. 1. Habit of *Isoëtes tegetiformans*. Triple plant with roots trimmed exhibiting seven microsporangia and distal, adventitious plantlets, × 3. [Drawing courtesy of Ms. Betsy Birkner, Staff Artist, Dept. of Botany, U.N.C., Chapel Hill]

Isoëtes tegetiformans Rury, sp. nov. **Figs. 1-8.**

Plantae amphibiae, sine cormis, tegetes formantes, plantulas distales adventitias saepe gerentes. Caulis prostratus, centraliter sulcatus, 3-35 mm longus, 0.5-1.5 mm diam., saepe deorsum tortus vel curvatus; radices non dichotome furcatae, plerumque in seriebus tribus linearibus secus sulcum medium utrinque dispositae: radices duae graciles laterales et una crassa (saepe spiralis) basalis una cum quoque folio consociatae; folia pauca (4-8), disticha, subulata, 2-4 cm longa, basi 1 mm lata et equitantia, filis peripheralibus absentibus, stomatibus secus partem folii tertiam supremam dispositis, ligula minus quam 1 mm longa, triangulari, velo perfecto; megasporangia elliptico-reniformia, ca. 1 mm longa, megasporis paucis (4-20), 275-370 μm diam., triletis, demisse tuberculatis, brunneis; microsporangia elliptico-reniformia, ad 1 mm longa, microsporis multis, 26-33 μm longis, monoletis, spinulosis, brunneis.

TYPE: Heggies Rock, 3.8 mi E from Columbia Junior High School along Georgia Rte. 232 and County Road 2122, Columbia County, Georgia, 110 m elev., 33°32′30″N Lat., 82°15′05″W Long., 21 Jan 1978; solitary, dense, mat-forming population growing in a 2-4 cm thick layer of fine, siliceous soil in a S-facing pool ca. 20 m^2 and 30 cm deep containing water with a circumneutral pH, *P. M. Rury & M. Treiber 259* (NCU; isotypes B, BH, DUKE, F, GA, GH, K, KYO, MASS, MICH, NY, UNCC, US).

This unique, mat-forming population of *Isoëtes* occurs in the largest of many pools on a 90-acre granitic flatrock. This pool is unique among the pools at Heggies Rock with respect to its location, aspect, size, structure, and resultant soil and water depths: The *Isoëtes* population dominates this large pool, nearly to the exclusion of other vascular plants, by virtue of its vegetatively reproductive, mat-forming (''tegetiformans'') growth habit.

The individual plants possess a slender, centrally furrowed, prostrate axis ca. 1 mm thick which exhibits bidirectional, intercalary-extension growth from the median furrow. The resultant axes are 3–35 mm long and possess both a linear phyllo- and rhizotaxis. The shoot apical meristem overlies the median furrow and develops typical *Isoëtes* leaves and sporophylls that are distichously disposed. However, unlike all other members of the *Isoëtaceae* and vascular plants in general, this shoot apex produces no cauline vascular tissue or vertical (primary) growth of the axis, and apparently has been reduced to a mere phyllogenic role. This type of distichous phyllotaxis and concomitant anatomy have been described by Paolillo (1963, p. 17) as a juvenile stage in *Isoëtes* corm development which typically persists only for the first 10–15 plastochrons of the young sporophyte.

The rhizotaxis of these plants is distinctly tristichous, a feature previously reported only for the genus *Stylites*, with two lateral rows of slender roots emerging proximal to the insertion of the leaf bases and one basal row of stout, often coiled roots which emerge proximal to the median furrow along the bottom of the axis. The roots of all specimens examined exhibit typical *Isoëtes* root anatomy but, as in *I. triquetra* and *Stylites*, are devoid of dichotomous branching. Usually three roots are produced per leaf, one from each row, and the resultant leaf-root complex becomes displaced along the axis and apparently becomes senescent as a unit. Developmentally, these three roots arise endogenously from a tracheary plexus in the vascular continuum, from which the single leaf trace departs to the associated, superadjacent leaf. This structural and developmental relationship between the roots and leaves of *I. tegetiformans* supports the contention of Liebig (1931) that the roots of *Isoëtes* are actually adventitious, as in other vascular cryptogams where roots arise in association with leaves.

The vasculature of the axes consists entirely of a sympodium of leaf and root traces which is continuous across the median furrow. The vasculature of these plants, therefore, supports the argument of both Farmer (1890) and Stokey (1909) that the vascular tissues of the *Isoëtes* stem represent a sympodium of leaf traces and that there is no true cauline portion to the stele. This sympodium, its ensheathing stem tissue, and the associated leaf-root complexes are displaced bidirectionally as a result of the sub-apical, intercalary-extension growth from the

median furrow. The occurrence of a "typical" isoëtaceous cambium in the region of the median furrow suggests that the intercalary growth results from cell divisions of this cambium that are restricted to the plane of the furrow. The often contorted morphology of the prostrate axes may be the result of differential cambial activity and/or the crowded conditions of their microhabitat. Additional study of this phenomenon is clearly necessary.

FIG. 2. Habit of *Isoëtes tegetiformans*. Double and triple plants with roots trimmed. Note the pair of distal, adventitious plantlets in the plant on the right. Scale is in centimeters.

Adventitious buds which develop into daughter plantlets are found distally on the axes at an observed minimum of 1-2 mm from the parental "leaf-producing apex." These buds arise *de novo* from the cauline storage parenchyma and form a vascular continuum that is identical to, but *non*-contiguous with, that of the parental axis. This bud formation potential is exemplified by the regeneration of seemingly dead stem fragments and by the remarkable ability of the entire population to survive repeated summer droughts and to revegetate after the water supply is replenished.

Sexual reproduction in this new species is typically isoëtaceous, and the adaxial sporangia, which do not exceed 1 mm in breadth, are completely covered by a subligular velum. The phenology of these plants apparently is seasonal, with microspores being produced in the winter-spring months and megaspores being produced in the summer-fall months. Although microsporogenesis was not observed, mature microsporangia were seen to contain numerous, brown, spinulose microspores 25-31 μm long. Megasporogenesis is typically isoëtaceous and begins

with the formation of four separate megasporocytes. Four to twenty megaspores were observed per sporangium; these exhibit a low-tuberculate sculpture, are dark brown, and are 275-370 μm in diameter. The occurrence of numerous young sporelings of typical *Isoëtes-Stylites* morphology indicates that sexual reproduction is successful within the population.

Isoëtes tegetiformans exhibits a combination of characteristics that is unique among the known species of Isoëtaceae, namely: sexual maturity in permanently distichous plants; a shoot apex which produces leaves and sporophylls only; a tristichous rhizotaxis of demonstrably adventitious roots; unbranched, frequently dimorphic roots; sympodial stem vasculature; a prostrate, intercalary growth habit; and the formation of cauline, adventitious buds.

TABLE 1. COMPARATIVE FEATURES OF *I. tegetiformans* AND *I. melanospora*.

Character	*I. tegetiformans*	*I. melanospora*
Population structure	Dense, mat-forming	Solitary, non-gregarious
Juvenile morphology and anatomy	Fixed "neoteny"	Environmentaly induced "neoteny"
Adventitious buds	Cauline	Absent
Root morphology	Non-dichotomizing, frequently dimorphic	Profusely dichotomizing, consistently isomorphic
Sporangia width	Up to 1 mm	1-2 mm
Velum coverage	Consistently complete	Complete to slight
Megaspores per sporangium	4-20	8-32 (greater for plants assignable to *I. piedmontana*)
Megaspore size	275-370 μm	350-480 μm
Megaspore sculpturing	Low tuberculate	Tuberculate to ridges
Microspore length	26-31 μm	25-30 μm
Microspore sculpturing	Spinulose	Smooth to papillate

Although unique with respect to this combination of features, this new quillwort can readily be recognized as a member of sect. *Tuberculatae* (*sensu* Pfeiffer, 1922) on the basis of its megaspore sculpture. It is interesting to note that the South American *Stylites* (2 spp.) and *I. triquetra* (the *Stylites-Isoëtes* intermediate) also are assignable to this section and are the only members of the Isoëtaceae which resemble *I. tegetiformans* in possessing non-dichotomizing roots. Within sect. *Tuberculatae*, *I. tegetiformans* is most similar to the members of the *I. melanospora* Engelm. complex of the southeastern United States. Unbranched specimens of *I. tegetiformans* are superficially similar to those of the incompletely described *I. melanospora* on the basis of plant size, distichous leaf arrangement, degree of velum coverage, and megaspore features. However, upon closer comparative study, a clear distinction between these two granitic endemics becomes apparent (see *Table 1*).

Isoëtes melanospora was originally described by Engelmann (1877, p. 395) from Stone Mountain, a large granitic dome in DeKalb County, Georgia. Engelmann described this Quillwort as a distichous plant with a compressed, bilobed corm inhabiting muddy pools at the summit of the granitic dome. The major reproduc-

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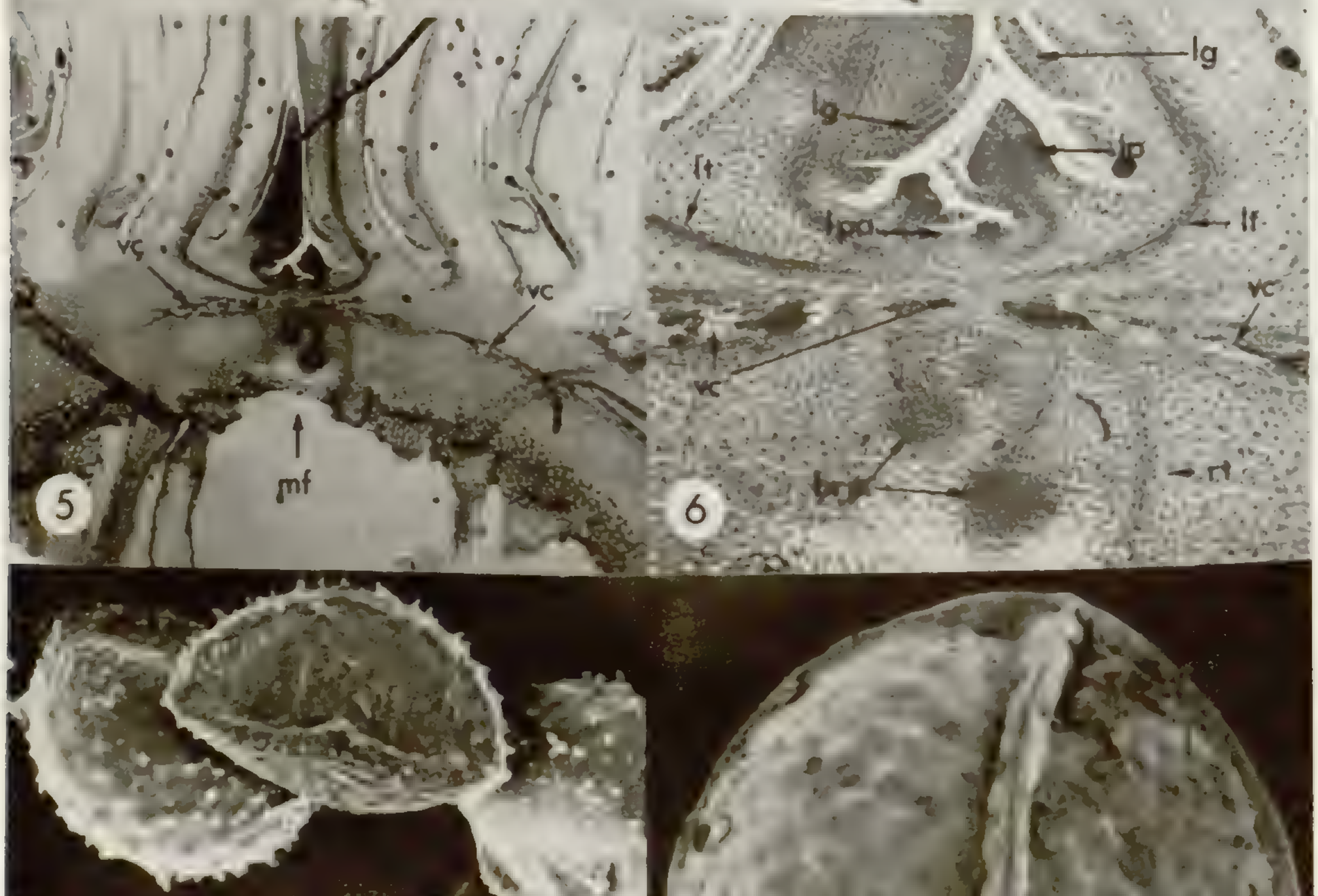
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tive features considered diagnostic for this species are sporangia completely covered by the subligular velum and black, tuberculate megaspores. Subsequent to its discovery, *I. melanospora* has been collected from several additional sites on the granitic flatrocks of the southeastern Piedmont.

In his revision of the Isoëtaceae of the southeastern United States, Reed (1965) included a species, *I. piedmontana* (Pfeiffer) Reed, which is closely related to and sympatric with *I. melanospora*. It is interesting to note in this regard that the narrow range of the granitic *I. melanospora* is included within the much broader range of *I. piedmontana*, a ubiquitous southeastern species which frequently inhabits the peripheral seepage areas and deeper soils (in pools) of these granitic outcrops. Subsequent comparative ecological and morphological study of *I. melanospora* and *I. piedmontana* has revealed the complete morphological intergradation of these two species (Matthews & Murdy, 1969). Furthermore, these authors uncovered a direct correlation between microhabitat features and the observed morphological intergradation of the populations investigated. Within a single population, they discovered that the smaller, distichous *I. melanospora* individuals are restricted to the shallower soils, whereas the larger, spiral-leaved ("typical") specimens of *I. piedmontana* consistently inhabit the areas with greater soil depths. These authors suggested that introgression of these two sympatric species might be responsible for their morphological intergradation. They apparently did not consider the possibility that these two "species" might actually represent different ontogenetic phases of the same species.

The neglect of developmental evidence in isoëtaceous taxonomy has been acknowledged by Reed (1965), who stated that "no attempt has been made to collect any one species in various phases of its growth from the same colony." I have observed both spiral and distichous individuals that are clearly assignable to *I. melanospora* (*sensu* Engelmann, 1877) within single populations at Stone Mountain and at Mt. Arabia, both in DeKalb County, Georgia. Distichous specimens were collected from both localities for comparative, uniform-environment growth studies in the laboratory. In 4-6 weeks, all of the distichous specimens from Stone Mountain and a majority of those from Mt. Arabia increased in stature and attained a spiral phyllotaxis characteristic of *I. piedmontana* and all other "typical," sexually mature Isoëtaceae. These observations, along with those of Matthews & Murdy (1969), strongly suggest that the distichous, juvenile form (*sensu* Paolillo, 1963) of *I. melanospora* merely represents an

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FIGS. 3-8. Morphology and anatomy of *Isoëtes tegetiformans*. FIG. 3. Triple, root-trimmed plant, following one year of "optimal" indoor cultivation, with two distal, adventitious plantlets, × 1.4. FIG. 4. Same as *Fig. 3*, with arrows indicating the daughter plantlets, × 3. FIG. 5. Median longitudinal section of an entire plant, at right angles to the median furrow (mf). Note the distichous phyllotaxis and the vascular continuum (vc), × 6. FIG. 6. Detail from *Fig. 5*. Note the leaf producing apex (lpa), leaf primordium (lp), ligule (lg), and the primordia of basal roots (brp). The leaf traces (lt) and root traces (lg) are components of the vascular continuum (vc), × 15. FIG. 7. Scanning electron micrograph of several monolete, spinulose microspores, × 700. FIG. 8. Scanning electron micrograph of a trilete, low-tuberculate megaspore, × 87.

arrested (neotenic) stage in the development of plants assignable to *I. piedmontana*. Although the present evidence seems convincing, further comparative biological studies of additional populations of these two "species" are desirable in order to confirm their synonymization. Nevertheless, it can be concluded that *I. melanospora* is not a strictly distichous species, as originally described by Engelmann (1877), and thus is in need of redefinition.

Having clarified reasonably well the morphological nature of *I. melanospora* and *I. piedmontana,* a clear distinction between *I. tegetiformans* and *I. melanospora sensu lato* can be made. *Isoëtes tegetiformans* resembles the distichous phase of *I. melanospora* with respect to plant size, leaf arrangement, and reproductive features. However, *I. tegetiformans* can be distinguished easily on the basis of its dense population structure; growth habit, stem morphology and anatomy, permanent distichy, unbranched, often dimorphic roots, and cauline adventitious buds. A comparison of the characteristics of *I. tegetiformans* and *I. melanospora* is presented in *Table 1.*

It is evident that the distichous, prostrate habit shared by these two granitic quillworts is merely the result of a neotenic convergence in form that is temporary in *I. melanospora* but permanent in *I. tegetiformans*. Indoor cultivation of the latter species for more than 18 months under the same growing conditions experienced by specimens of *I. melanospora* resulted in no significant morphological changes. This suggests that the neotenic form of *I. tegetiformans* is an immutable, species-specific characteristic, whereas a similar neotenic phenomenon in *I. melanospora* merely results from microhabitat influence upon the stature and correlative degree of pre-sexual morphological development of the individuals. In addition to being a fixed neotenic form, *I. tegetiformans* is also very distinct from *I. melanospora* (and all other North American species of *Isoëtes*) in having non-dichotomizing, frequently dimorphic roots and in forming numerous cauline, adventitious buds (plantlets). Beyond such general considerations, however, the precise nature of the relationship between *I. tegetiformans* and *I. melanospora* is enigmatic, and probably shall remain so until a thorough systematic study and taxonomic revision of the entire *I. melanospora* complex is completed.

The factors causing the unique morphology of this plant are presently conjectural and require further investigation. However, Lammers (1950) revealed that individuals of *I. melanospora* subjected to full sunlight at ca. 10,000 ft-c exhibit a photosynthetic rate nearly twice that of their dark respiration rate. If the photosynthetic response curve and relative rate of dark respiration are comparable for *I. tegetiformans*, then the prolific growth habit of this species is easily understood in terms of its physiology and microhabitat. The pool it inhabits is south-facing, sheltered on the north flank, and has a maximum soil and water depth that apparently is maintained by a natural, south-facing spillway from the pool. Throughout the evolutionary development of the species, this spillway may have prevented the accumulation of soil within the pool to such a degree that soil depth limited the potential stature of the plants. The long-term effect of such restrictions on plant stature, along with a potential optimal photosynthetic efficiency, may be responsible for the unique morphology and prolific growth habit of this Merlin's-grass.

Therefore, this spreading, carpet-forming species might best be regarded, evolutionarily, as an *Isoëtes* which "grew-out" like a grass instead of "growing-up" like a Quillwort.

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REVIEW

"TENTAMEN PTERIDOPHYTORUM GENERA IN TAXONOMICUM ORDINEM REDIGENDI," by R. E. G. Pichi Sermolli, Webbia **31:** 313-512. 1977.—Professor Pichi Sermolli has written a most detailed and exhaustive treatment of fern classification down to the level of genus. His treatment is illustrated with a table of families and tree-like diagrams of the genera or groups of genera within each family, and includes a conspectus of the families and genera with generic numbers allowing for intercalation of additional genera, an index of the genera and their synonyms, and discussions of the genera and their characteristics.

In contrast to most linear arrangements of genera proposed in the past, Pichi Sermolli's treats all the genera of a single line of evolution from primitive to advanced before passing on to another line of evolution. In my opinion, this is a more natural and satisfactory method than is treating first all primitive genera and then all advanced ones, regardless of which of several phyletic lines they belong to.

His classification groups 443 genera of living pteridophyta into 64 families—both record high numbers. Many of the genera I consider subgenera at best. Judging by the lengthy discussion of the genera, Pichi Sermolli gives more weight to certain differences in morphology than do most authors; he is a self-admitted splitter.

There is one good reason for such splitting in proposing a classification: it forces users to consider the differences between finely split genera which otherwise might be ignored. The disadvantage is that in using one level of classification rather than two (genus and subgenus), Pichi Sermolli's classification contains less information about relationships of genera within his families. Fortunately, his tree-like diagrams convey this information, although his conspectus and any herbarium arrangement based on it would not. Whether one adopts finely split genera or more comprehensive ones is to some extent a matter of personal preference or need, but either way Pichi Sermolli's work will be very useful for a long time to come.—*D.B.L.*

State and Local Fern Floras of the United States, Supplement II

MERYL A. MIASEK*

This list continues the two publications of S. F. Blake (Amer. Fern J. **31:** 81-90, 131-143. 1941; **40:** 148-165. 1950) to bring to the attention of JOURNAL readers recent Floras, manuals, and checklists dealing with ferns and fern-allies of the United States. Supplement II covers the years 1950-1977. The list is organized alphabetically by state and author, with regional works at the end. Mimeographed lists and other ephemera are excluded. Works dealing with Canadian ferns are represented only when pteridophytes of the United States also are treated. Many short papers dealing with range extensions and locality records also are excluded; some of these are given in a list titled "Regional, State and Local Fern Floras, Manuals, Checklists and New Fern and Fern-ally Records for the U.S. and Adjacent Canada, Since 1950," which I compiled. This list is available from the Library of the New York Botanical Garden, Bronx, NY 10458.

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SHORTER NOTES

ATHYRIUM FILIX-FEMINA NEW TO SASKATCHEWAN.—In eastern North America, the Northern Lady Fern, *Athyrium filix-femina* var. *michauxii* (Spreng.) Farw., reportedly ranges from central Labrador, Newfoundland, Nova Scotia, and Maryland westward to central and southeastern Manitoba, South Dakota, and Missouri. This variety overlaps and apparently intergrades with the Southern Lady Fern, *A. filix-femina* var. *asplenioides* (Michx.) Farw., which extends from Florida and western Texas northward to New England, New York, Pennsylvania, West Virginia, Kentucky, Indiana, Missouri, and Oklahoma. Variety *michauxii* has been separated by a gap of 700 miles or more from the Western Lady Fern, *A. filix-femina* var. *sitchense Rupr. (syn.* subsp. *cyclosorum* (Rupr). C. Chr.), which ranges from southern Alaska to northern Mexico and eastward to western Alberta, Montana, the Dakotas, Nebraska, Colorado, and New Mexico. When considered as subsp. *cyclosorum,* a southern ecogeographical var. *californicum* Butters has been distinguished by some authors. In Canada, the midcontinental gap which has been apparent between the Northern and the Western Lady Fern has been thought to extend from central Manitoba across Saskatchewan to westernmost Alberta.

Recently we discovered var. *michauxii* at four separate localities in northeastern Saskatchewan. The collection data are as follows: 14 mi. W of Numabin Bay of Reindeer Lake, mile 1.25 of Highway 105 (Wollaston Lake Road), 56°16′N Lat., 103°36′W Long., lush white birch/river alder/willow woods along stream, *Ternier & Jasieniuk 2113* (SASK); 3.5 mi. N of Courtenay Lake, mile 98 of Highway 105, 57°30′N Lat., 103°58′W Long., moist white birch woods at creek mouth, *Ternier & Jasieniuk 1420* (SASK); 5 mi. S of Geikie River bridge, mile 110 of Highway 105, 57°37′N Lat., 103°54′W Long., moist white birch woods along small creek, *Ternier & Jasieniuk 2352* (SASK); and Parks Lake inlet to Hidden Bay of Wollaston Lake, 58°08′N Lat., 103°41′W Long., lush, moist gallery white birch/black spruce/river alder mixed woods, *Harms 21605, 21606* (SASK), *Harms & Wright 23757* (SASK). The plants were common to moderately abundant at each of these sites.

These collections represent the first records of *A. filix-femina* in Saskatchewan and constitute a northwestward range extension of approximately 250 miles for var. *michauxii* from its known occurrence at Swampy Lake on the Hayes River in central Manitoba. Since the present range extension is northwestward, rather than due west, it is largely parallel to the eastern limit of var. *sitchense* in the Rocky Mountains, and so the apparent gap between the Northern and Western Lady Ferns in Canada remains at over 600 miles.

The sterile fronds of the Saskatchewan specimens seem remarkably similar to those of the Spinulose Shield Fern, *Dryopteris austriaca* (Jacq.) Woynar var. *spinulosa* (Muell.) Fiori, one of our more common boreal ferns, and could easily be confused with it. In my opinion, the likeness is more apparent in the Sas-

katchewan specimens than it is in specimens from eastern Canada and the United States. I suspect that the Lady Fern may have been overlooked previously in Saskatchewan and western Manitoba by collectors who mistook it for *D. austriaca*. However, an apparently consistent vegetative character to distinguish the two is the venation of the pinnules. In *Athyrium*, the veins reach the pinnule margin, whereas in *Dryopteris* they stop short and end in elongate hydathodes that are best seen on the adaxial surface of the frond.—*Vernon L. Harms, Fraser Herbarium, Department of Plant Ecology, University of Saskatchewan, Saskatoon, Sask. S7N 0W0, Canada.*

NEW COMBINATIONS IN THE FERN FLORA OF VENEZUELA.—While we were revising a checklist of the ferns of the state of Mérida, Venezuela, we found some entities that needed a new combination or a new name. The nomenclatural changes for these are as follows:

Lycopodium nesselianum Duek & Lellinger, nom. nov.

Urostachys moritzii Nessel, Rev. Sudam. Bot. **6:** 160, *t. 9, f. 29*. 1940, *non Lycopodium moritzii* Muell. Bot. Zeit. **19:** 65. 1861. HOLOTYPE: Sierra Nevada, Venezuela, *Greven 61* in 1898 (not seen).

Trichomanes radicans var. kunzeanum (Hooker) Duek & Lellinger, comb. nov.

Trichomanes kunzeanum Hooker, Sp. Fil. **1:** 127, *t. 39D*. 1844. SYNTYPES: Pangoa, Depto. Junín, Peru, *Mathews 1088* (K not seen Morton photo 19051); Pampayacu, Depto. Huánuco, Peru, *Poeppig* (K not seen); and Caracas, Distr. Fed., Venezuela, *Linden 176* (K not seen; isosyntype FI not seen Morton photo 16586). The isosyntype is labelled "Hautes Andes de Truxillo et de Mérida."

Grammitis amphidasyon (Kunze ex Mett.) Duek & Lellinger, comb. nov.

Polypodium amphidasyon Kunze ex Mett. Abhandl. Senckenb. Naturforsch. Gesell. **2:** 49. 1856. SYNTYPES: Mérida, Edo. Mérida, Venezuela, *Funck & Schlim 959* and *1100* (both B neither seen).

Grammitis gameriana (Vareschi) Duek & Lellinger, comb. nov.

Polypodium gamerianum Vareschi, Acta Bot. Venez. **1:** 117, *f. 16*. 1966. Cerca de Laguna de los Anteojos, Edo. Mérida, Venezuela, 4100 m elev., *Vareschi & Maegdefrau 6839* (VEN).

Grammitis xanthotricha (Klotzsch) Duek & Lellinger, comb. nov.

Polypodium xanthotrichum Klotzsch, Linnaea **20:** 376. 1847. SYNTYPES: Mérida, Edo. Mérida, Venezuela, *Moritz 250?* (B not seen); and Guyana, *Rich. Schomburgk 1172* (B not seen).

Elaphoglossum mortonianum Duek & Lellinger, nom. nov.

Acrostichum attenuatum Kunze, Linnaea **36:** 56. 1869, *non* Fée, Icon. Esp. Nouv. [Mém. **6**] 1, *t. 1, f. 1*. 1853. SYNTYPES: Mérida, Edo. Mérida, Venezuela, *Funck & Schlim 970* (LZ destroyed); Colonia Tovar, Edo. Aragua, Venezuela, *Moritz 125* (LZ destroyed), *441* (LZ destroyed; isosyntype BM not seen Morton photo 7129), and *Fendler 290* (LZ destroyed; isosyntypes US, Y not seen photo at US).

J. J. Duek, CIDIAT, Universidad de Los Andes, Apartado Postal 219, Mérida, Venezuela, and *David B. Lellinger, U.S. National Herbarium, Smithsonian Institution, Washington, DC 20560.*

TRISMERIA. . .TRIFOLIATA?—Since having been described in 1753 by Linnaeus as *Acrostichum trifoliatum,* the Split-pinna Fern, as Wherry called it in his "Southern Fern Guide," was segregated into its own genus *Trismeria* by Fée in 1852, and more recently was transferred to *Pityrogramma* by Tryon (Contr. Gray Herb. **189:** 68. 1962), who also indicated that the pinnae may be simple or 2- to 7-foliolate.

During a population sampling, mass field collections were made for flavonoid analysis and it was observed that the typical form, with 3-foliolate pinnae, was scarcely represented in the collections compared to other types of pinnae. A total of 4716 fronds from twelve populations made from sea level to 1,200 m altitude along the Caribbean-facing side of Costa Rica were examined. Percentages of the pinna types were as follows: 25.1696% simple; 55.1738% 2-foliolate; 18.7234% 3-foliolate; 0.9329% 4-foliolate; and none 5- to 7-foliolate. Trend analysis to establish a possible correlation between frequency of x-foliolate pinnae along an altitudinal gradient proved negative.

TABLE 1. DISTRIBUTION OF PINNA TYPES IN FIVE *Trismeria trifoliata* POPULATIONS.

Population	*1-foliolate*	*2-foliolate*	*3-foliolate*	*4-foliolate*	*5-foliolate*	*6-foliolate*	*7-foliolate*
A	25.9825	45.8515	27.5109	0.6550	0.	0.	0.
B	17.1521	35.2750	33.6569	13.5922	0.3236	0.	0.
C	28.1833	50.0848	19.6943	1.5280	0.1697	0.1697	9.1697
D	17.0774	75.0000	6.8661	1.0563	0.	0.	0.
E	20.0000	45.3333	29.8666	4.8000	0.2666	0.	0.

Another set of five populations growing at 800-1,200 m elevation in the Meseta Central of Costa Rica was sampled. The results from 2608 fronds are shown in *Table 1.*

Linnaeus apparently chose the epithet *trifoliatum* because of the generally trifoliolate condition of the frond illustrated in plate 45, figure 2 of Sloane's "Voyage." However, this generalized condition certainly is not the case in Costa Rican material.

The composition of the farina deposited on the undersurface of fertile *T. trifoliata* pinnae is very similar to that of *Pityrogramma calomelanos* and some other species of this genus (Wollenweber, E. 1976. Zeitschr. Pflanzenphysiol. **78:** 344-349). The main component is a dihydrochalcone, which is accompanied by varying amounts of minor flavonoids, some of which are new products (V. Dietz, unpubl.). A detailed analysis of *T. trifoliata* population samples has not yet been accomplished, but our impression is that only rather small variations of a mostly quantitative nature occur. Such variations can be observed in *P. calomelanos* even on different fronds of one plant Hence, it obviously would be idle to search for correlations between farina composition and pinnule number in *T. trifoliata.*—*Luis Diego Gómez P., Herbario Nacional, Museo Nacional de Costa Rice, Apartado 749, San José, Costa Rica* and *Eckhard Wollenweber, Technische Hochschule Darmstadt, D-6100 Darmstadt, Federal Republic of Germany.*

REVIEW

"FERNS OF HONG KONG," by Harry H. Edie. xvii + 285 pp. Hong Kong University Press, 1978. ISBN 962-209-002-8. HK$40.00 (Ca. US$8.00).—This paperback book is a comprehensive introduction to the ferns (but not fern allies) of Hong Kong, Kowloon, and the New Territories. It is the only account of the ferns published for the region in over 50 years, and so is indispensible, especially because it incorporates the most recent generic concepts and alignments. The introduction is useful for beginning students of ferns; the part on fern ecology is especially interesting. The taxonomic part of the book includes keys, descriptions, distributions, and notes on the species. Synonyms are listed in a separate checklist that provides a useful overview of the colony's ferns. Many of the species are illustrated with the author's own line drawings. A glossary, a list of Chinese names for the ferns, and an index conclude the volume. This work is highly recommended for amateur and professional students of Asiatic ferns.—*D.B.L.*

AMERICAN FERN JOURNAL

Manuscripts submitted to the JOURNAL are reviewed for scientific content by one or more of the editors and, often, by one or more outside reviewers as well. During the past year we have received the kind assistance of J. G. Bruce, C. Haufler, R. L. Hauke, R. M. Lloyd, J. Montgomery, R. Oliver, G. R. Proctor, J. E. Skog, A. R. Smith, R. G. Stolze, W. C. Taylor, J. Utley, and R. A. White, to whom we are deeply indebted. We welcome suggestions of other reviewers and offers of assistance.—*D. B. L.*

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ERRATA

P. 23, line 12. For "*chryosophylla*" read "*chrysophylla.*"
P. 33, title. For "Selanginella" read "Selaginella."
P. 78, line 48. For "*furcata*" read "*furcatum.*"
P. 79, line 2. For "*tepuiensis*" read "*tepuiense.*"
P. 79, line 5. For "*acuminata*" read "*acuminatum.*"

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Equisetum ramosissimum in North America

RICHARD L. HAUKE*

Equisetum ramosissimum Desf. is widely distributed in the Eastern Hemisphere, ranging through southern, eastern, and mediterranean Africa, the Canary and Azores islands, Europe north to southern Germany, and Lithuania and east through the Balkans and Asia Minor to Mongolia, Korea, and Japan. A subspecies, *E. ramosissimum* subsp. *debile* (Roxb.) Hauke, is found in India, southeastern Asia, and the south Pacific Islands to Fiji.

This species is a member of subg. *Hippochaete* and, as the specific epithet indicates, is much branched, unlike most of the other members of the subgenus. It is also unlike them in often having double or triple lines of stomata between the ridges along the stems. In these characters it can readily be mistaken for *E. giganteum*, *E.* × *schaffneri*, or, when with only single lines of stomata, *E. myriochaetum*.

As with other species of *Equisetum*, *E. ramosissimum* subsp. *ramosissimum* is variable (Milde recognized 34 varieties). In addition to the species mentioned above, it also can be mistaken for *E. hyemale*, *E. laevigatum*, *E.* × *ferrissii*, or *E.* × *moorei* (in Europe). But the combination of regular branching, long internodes, long sheaths, brownish sheath coloration with a black girdle, flattened sheath segments, persistent but shriveling sheath teeth, often multiple lines of stomata, prominent vallecular and carinal collenchyma, silica surface with numerous pilules, and green spores tends to distinguish this species from all the others, which may show one or more of the above characters, but not most or all of them.

Under the distribution of *E. ramosissimum*, Milde (1867, p. 461) listed "British Columbia 49° n Br. (Dr. Lyall)." Since there has been no further record of this species in North America, it has not been included in the flora of North America. In the last few years, however, a few collections from North America have come to my attention:

NORTH CAROLINA: New Hanover Co.: Dense population of branching plants on sandy ditchbank through ballast dump on east side of Northeast River, south of the old US-17 bridge, Wilmington, 22 Aug 1970, *S. W. Leonard 3557* (KIRI). Ditch and sand flats on ballast area, east side of Northeast River, Wilmington, 3 Sep 1970, *S. W. Leonard & A. E. Radford 3716* (TENN, KANU).

FLORIDA: Escambia Co.: Plants to 2.5 m tall, supported by thicket of wax myrtle and willow (much lower and unbranched in adjacent mowed field), continuous over broad field, moist to wet clayey soil, NW corner of Main and Donelson, S side of Pensacola, T2S, R30W, 24 Jun 1975, *D. B. Ward 8968* (FLAS, KIRI). Vigorous colony, on rich, black soil, with *Eupatorium*, *Ipomoea*, *Fumaria*, *Plantago*, *Rumex*, etc., at NW corner of Main St. and Donelson St., Pensacola, 2 May 1975, *J. R. Burkhalter 2254* (FLAS).

When Leonard sent me a specimen in August, 1970, he described it as evergreen, mostly branched, and at its reproductive peak, and he noted that the area was rich in European records. I wrote to him that it looked to me like *E.* × *ferrissii* (known from North Carolina), but because of the time of coning and presence of green spores, it must be an odd form of *E. hyemale* var. *affine*.

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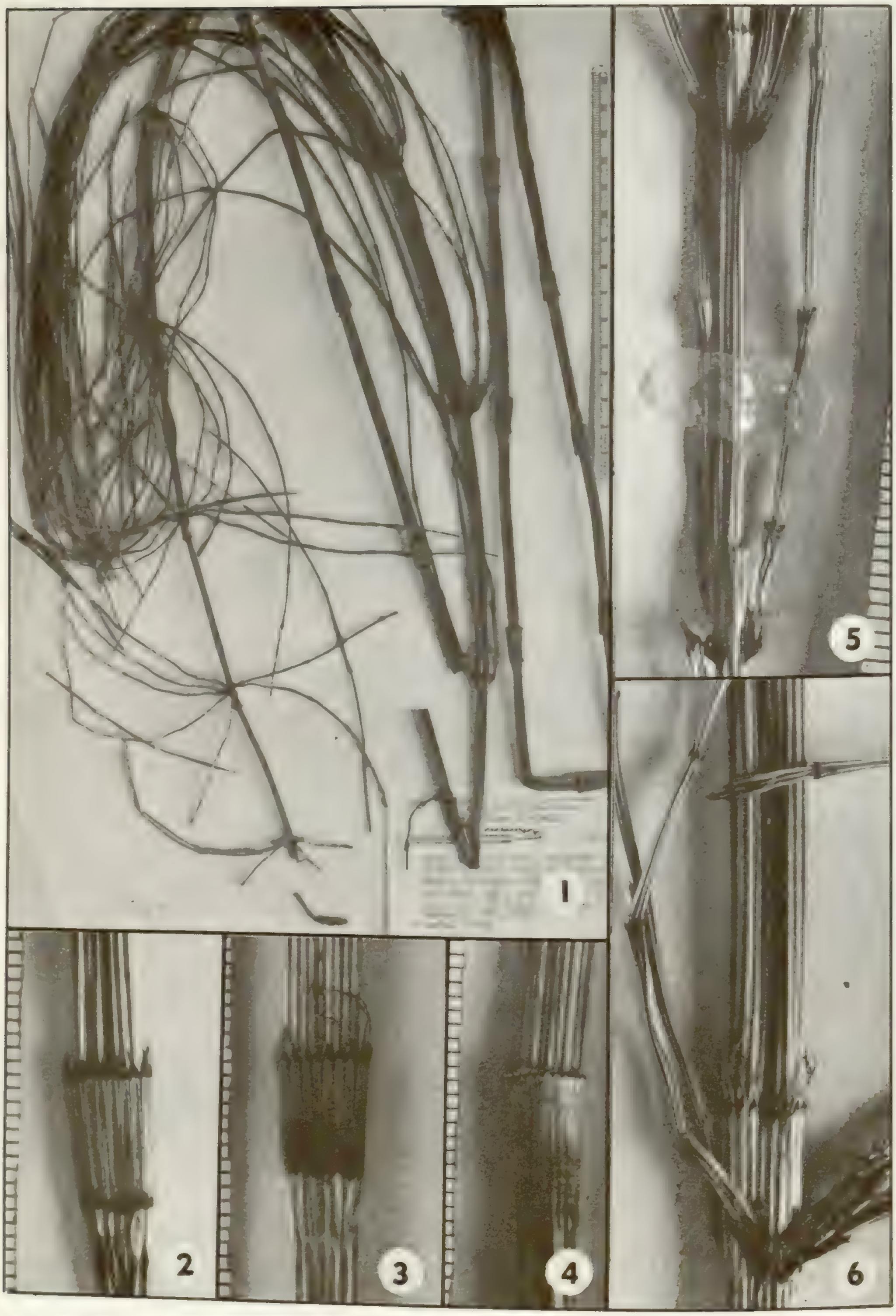


FIG. 1. Herbarium specimen of *Equisetum ramosissimum* Desf. from Florida, *Ward 8968* (KIRI). FIGS. 2–6. Nodal sheaths (mm scale included). FIG. 2. *E. ramosissimum*, Florida, *Ward 8968*. FIG. 3. *E. ramosissimum*, Jordan, *Hauke s.n. (KIRI)*. *FIG. 4. E.* × *ferrissii* Clute, Michigan, *Hauke 56* (KIRI). FIG. 5. *E. ramosissimum*, North Carolina, *Leonard & Radford 3716* (TENN). FIG. 6. *E. ramosissimum*, Jordan, *Hauke s.n.*

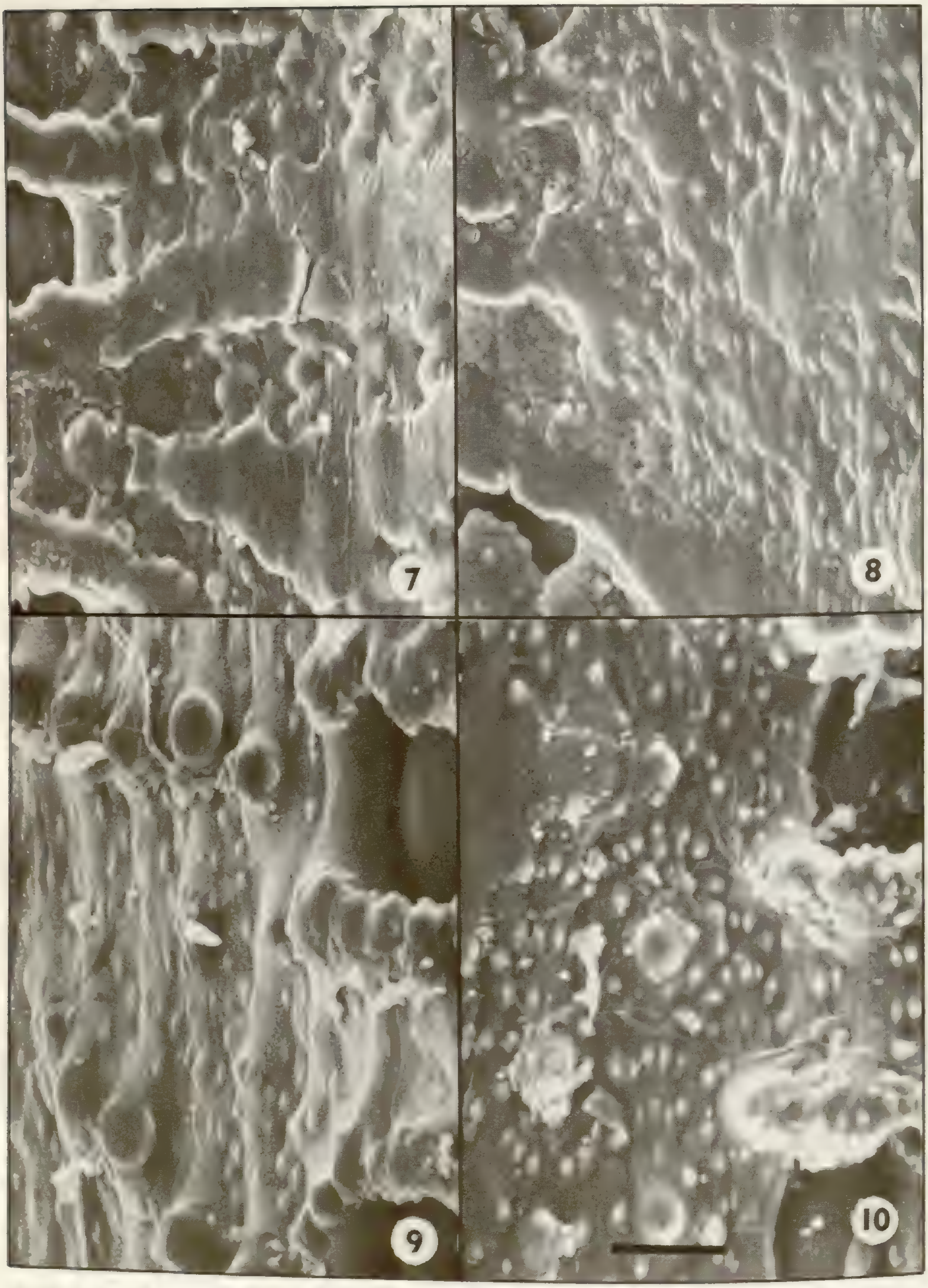
In June, 1975, Daniel Ward sent me some specimens of *Equisetum* collected in Florida. Most were obviously *E. hyemale* var. *affine*, but *Burkhalter 2554* appeared different. Ward wrote, "The area is fill, on the site of the ballast dumps of the early seaport, Pensacola having been during the heyday of the yellow pine days, the second most active port on the Gulf. The *Equisetum*, although seemingly reproducing only by vegetative means (no outlying stations are known), occurs on both sides of a 30 ft. paved road, suggesting a very early station since bisected." I identified the odd specimen as *E.* × *ferrissii* and commented on the excessive length of the internodes and sheathes. A later collection by Ward at the same station is illustrated *(Fig. 1)*.

A. Murray Evans sent me a specimen in January, 1978 of what he thought was *E. laevigatum* collected at Wilmington, NC by Leonard and Radford. At first it appeared to me to be *E.* × *ferrissii*, but the stomatal lines were frequently doubled, and this together with the green spores and regularity of branching made me realize that it represented *E. ramosissimum* subsp. *ramosissimum*.

Since *E. ramosissimum* and *E.* × *ferrissii (Fig. 4)* have similar internal anatomy and sheath appearance, I obtained scanning electron micrographs of the surface silica micromorphology to confirm this identification. *Equisetum ramosissimum (Fig. 9)* is characterized by having numerous pilules of silica over the surface, including the silica overarching the stomates. *Equisetum* × *ferrissii (Fig. 7)* has the surface pitted between transverse plates of silica, and completely lacks the pilules so characteristic of *E. ramosissimum*. The Wilmington *(Fig. 10)* and Pensacola *(Fig. 8)* collections display numerous pilules, thus confirming their identity as *E. ramosissimum*.

How can we account for the sudden appearance of *E. ramosissimum* subsp. *ramosissimum* in southeastern North America? The North Carolina locality suggests that it might have been brought in with the ballast many years ago and overlooked until recently. Vegetative transport of *Equisetum* with fill has been noted previously (Hauke, 1963, pp. 28–29). The presence of *E. ramosissimum* in Pensacola, also a seaport, could be similarly explained. However, for a number of years *Equisetum* was known from only one locality in Florida (*E. hyemale*, along the Appalachicola River), and it seemed unlikely that in a metropolitan area like Pensacola a population of *Equisetum* would have escaped detection for long. Ward and Burkhalter (1977) discussed another plant from the ballast area of Pensacola, *Acacia smallii*, a small tree collected in 1901 and 1903, then not again until they collected it in 1975. Of the area, they say, "The quantities of ballast have been leveled and distributed to fill much of the old harbor area, and warehouses, parks, and roadways are now scattered where once sailing ships were at anchor. But waste areas have persisted, and with them many of the early introductions." If a tree could escape detection in Pensacola for nearly three quarters of a century, it is not surprising that *Equisetum ramosissimum* also escaped detection until recently.

The possibility that *E. ramosissimum* is more widespread in North America than the two known localities cannot be denied. The occurrence of *E. ramosis-*



FIGS. 7–10. Scanning electron micrographs of *Equisetum* stem surfaces. FIG. 7. *E.* × *ferrissii*, Kansas, *Hartman 1090* (KIRI). FIG. 8. *E. ramosissimum*, Florida, *Ward 8968*. FIG. 9. *E. ramosissimum*, Jordan, *Hauke s.n.* FIG. 10. *E. ramosissimum*, North Carolina, *Leonard 3557* (KIRI). Scale line on FIG. 10 is 25 μm.

simum in the Pacific Northwest remains a distinct possibility. In an extensive survey of herbarium specimens from throughout North America, I never detected any *E. ramosissimum*. But since I did not at first recognize the two presently known populations as *E. ramosissimum*, that is not proof of its absence. However, I am confident that under conditions of systematic comparison of many specimens, I would have detected it if present, even though individual specimens sent at widely separate times were not immediately recognized.

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REVIEW

"A TAXONOMIC REVISION OF THE NEW ZEALAND SPECIES OF ASPLENIUM" and **"ASPLENIUM HYBRIDS IN THE NEW ZEALAND FLORA,"** by P. J. Brownsey, New Zealand J. Bot. **15:** 39-86, 601-637. 1977.—Because of its propensity to form interspecific hybrid complexes, *Asplenium* is a taxonomically troublesome genus everywhere it occurs. The species in New Zealand are no exception. Brownsey's revision is an excellent integration of classical taxonomy and cytotaxonomy. Besides a key to the species, synonymies, descriptions, statements of habitat and distribution, and comments, silhouettes and drawings of rhizome scales are given for each of the species, and all are mapped in detail. The photographs of spores taken through the light microscope are not so revealing as scanning electron microscope pictures would have been, but even so, obvious differences between some of the species can be seen. The revision treats 16 basic species and subspecies, and a crossing polygon shows hybridization between them. Especially *A. bulbiferum*, *A. flaccidum*, and *A. obtusatum* each form several different hybrids. Nineteen hybrids are described and illustrated. At least as many more other combinations also occur, but their characterization and analysis awaits further cytotaxonomic study. The species complexes, so far as currently known, are analyzed with genome diagrams. Brownsey sensibly has chosen to refer to the hybrids with formula names, rather than to coin new epithets. Since the number of possible hybrids is nearly infinite, it is best to use formula names for all hybrids except those that are unusually important because of their wide range, abundance, horticultural value, or role as parents of other hybrids.—*D.B.L.*

Notes on the Dispersion of Dryopteris Spores in the Great Dismal Swamp

THOMAS W. MAGRAW* and LYTTON J. MUSSELMAN**

During the past few years, considerable attention has been paid to *Dryopteris* in the Dismal Swamp. However, no studies on spore dispersion have been conducted in the swamp, although such studies are important in understanding the life histories of these ferns.

The Dismal Swamp contains a large number of plants of sexual *Dryopteris* species plus some hybrid plants (Nickrent et. al., 1978). The hybrids are of particular interest because some of them, like *D. celsa* × *cristata* are able to reproduce and so form large stands. In the hybrids, the production of giant spores, considered to be a form of apomixis, is well known (De Benedictis, 1969). In addition to giant spores, other abnormal spore types (diads, triads, and fused tetrads) are produced in a manner apparently similar to that described by Hickok and Klekowski (1973).

The objectives of this study were to examine the dispersion of spores within the fern's immediate habitat, to assess spore drift above the canopy, and to determine the dispersability of hybrid spores.

MATERIALS AND METHODS

The spore traps used in this study consisted of a 4.0 × 1.3 cm strip of double-stick transparent tape attached to one side of a microscope slide. The slides of ground-level traps were held with their long axis vertical just above the soil by the handle of bacteriological slide holders. Slides above ground level were positioned similarly by suspending the slide holders from a monofilament line placed 1.5 m above ground level so that the slides faced south. Pairs of traps were placed vertically and facing west on a fire tower at 5.33 m intervals starting just below the top of the tree canopy at 21.33 m above the ground. All of the spore traps actually may have under-collected fern spores, compared with the true number in the air. Other sampling machinery, e. g. "rotoslide samplers" (Raynor et al., 1976), may be more effective in trapping spores.

Spores were counted at two contrasting sites about 25 miles SSW of Norfolk, VA. A fire tower located in the Dismal Swamp National Wildlife Refuge was used to collect data from above and just below the tree canopy. No large *Dryopteris* populations occur within a mile of the tower. A ground-level station just south of U.S. highway 158 in Gates County, NC served to make ground-level observations. *Dryopteris* is the most abundant herbaceous plant at this site. Both *D. celsa* and its hybrid with *D. cristata* are present at this site.

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Dryopteris plants in the Dismal Swamp release their spores at slightly different times. *Dryopteris intermedia* is first, followed by *D. spinulosa*, *D. cristata*, and *D. celsa*. The peak of spore release by the latter species for the 1978 season was in the last week of June. Because of time limitations on our research, spore trapping began at that time and continued into August.

TABLE 1. AVERAGE DAILY SPORE COUNT PER CM² BETWEEN JUNE 27 AND JULY 1, 1978 FOR FIVE LOCATIONS 1.5 M DISTANT IN A STRAIGHT LINE.

Number of fronds/m²	*Ground level*	*1.5 m above ground level*	*Total*
15	34	0.14	34.14
12	4	0.34	4.34
1	1.2	0.24	1.44
0	9	0.53	9.53
0	4	0.53	4.53
Total	52.2	1.78	

Athyrium asplenioides, *Asplenium platyneuron*, *Osmunda cinnamomea*, and *Woodwardia areolata* all are very common throughout the swamp. Voucher slides of spores of each were made in order to identify spores on the traps accurately. *Dryopteris* spores were distinguished easily from other fern spores by their reniform shape and distinctive perispore.

TABLE 2. AVERAGE DAILY SPORE COUNT PER TRAP AT 1.5 M ABOVE GROUND AND AT GROUND LEVEL.

Spore type	*June 27-July 1*	*July 1-3*	*July 21-27*
	1.5 m above ground level		
Normal	10	8	6
Hybrid	0	0	0
Total	10	8	6
	0 m above ground level		
Normal	271	60	11.33
Hybrid	0	0	0.67
Total	271	60	12

Judging by the spore counts on traps set at the ground-level (*Table 1*), there is little vertical or lateral movement of fern spores from their point of origin. Most spores fall to the ground close to the fronds which produced them, presumably because of the relatively mild air currents within the dense forest. There is a rough correlation between frond density and the number of spores trapped. Relatively few spores are wafted into the air and caught on traps 1.5 m above ground level. It is possible that the results in *Table 1* are biased because the data were collected at stations spaced 1.5 m distant along a straight line, five at ground level and five 1.5 m above the ground. A grid pattern containing more stations might have been more revealing.

Hybrid spore dispersion is of particular interest since it has been suggested that *Dryopteris* hybrids like *D.* × *separabilis* may have invaded at least one of the study sites in the form of an unreduced giant spore (Nickrent et al., 1978). The present study indicates that hybrid spores are only infrequently collected (*Table 2*). This may be an indication of the low number of spores dispersed from hybrid plants, or perhaps giant spores are even more prone to fall directly beneath the plants that produced them than are normal spores.

TABLE 3. TOTAL COUNTS OF SPORES TRAPPED BELOW AND ABOVE THE TREE CANOPY IN THE DISMAL SWAMP.

Height above ground (m)	*July 7–14*	*July 14–21*	*July 21–27*	*July 29–Aug 5*	*Total*
42.67	0	1	—[1]	0	1
37.33	0[2]	5	2	0	7
32.00	0	1[2]	2	0	3
26.67	1[2]	0[2]	3	0	4
21.33	0[2]	—[1]	3[2]	0	3
Total	1	7	10	0	

[1]Both traps lost. [2]One trap lost.

A small number of spores do manage to drift on air currents above the tree canopy, clearing it by even as much as 18.29 m (*Table 3*). The top of the canopy is about 24.38 m above the ground. There appears to be no significant difference in the number of spores trapped at any level between 21.33 and 37.33 m. About 60% of the fern spores recovered from the fire tower traps were not *Dryopteris*, which is reasonable because large populations of *Athyrium asplenioides*, *Osmunda cinnamomea*, *O. regalis*, *Woodwardia areolata*, and *W. virginica* are nearby.

Future studies should be conducted over the entire sporulating season and beyond to examine more carefully the presence of spores carried high in the air. Likewise, traps should be set at various distances from the main *Dryopteris* centers within the swamp. Additional work also is needed on the number and types of viable spores produced by hybrids, as well as their dispersion in the air.

This work was supported by NSF grant SMI-76-0123. Preliminary collections were made by Ms. L. A. Pitchford and were supported by a grant from the National Geographic Society.

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An Artificial Crossing Technique for Selaginella

TERRY R. WEBSTER*

Various methods for obtaining microgametophytes, megagametophytes, and sporelings of *Selaginella* have been described. Slagg (1932), in a study of microgametophyte development in *S. kraussiana* (Kunze) A. Br., germinated microspores on plaster of Paris blocks. A similar method for germinating both microspores and megaspores was described by Bold (1967). Bierhorst (1964) described methods for obtaining reproductive stages of *Selaginella* for classroom use. Webster (1967) described the induction of sporelings under greenhouse and field conditions. Wetmore and Morel (1951) germinated megaspores of *S. pallescens* (Presl) Spring in Mart. and *S. flabellata* (L.) Spring on nutrient agar under sterile conditions. Through the use of a medium supplemented with various growth factors, they were able to grow gametophytic tissue for several months.

Despite the above procedures for germinating spores and obtaining sexual material of *Selaginella*, there is but one report of artificial crosses in the genus. Burgeff and Filippi (1957) made crosses between *S. martensii* Spring var. *martensii* and *S. martensii* var. *variegata* Hort. They sowed surface-sterilized megaspores and microspores together on nutrient agar in culture tubes and, after gametophytes had formed, flooded the cultures with water to achieve fertilization. After 30–40 days, sporelings appeared. Using this method, they studied the inheritance of variegation in *S. martensii* var. *variegata*.

In this paper, a crossing technique differing in several respects from the one used by Burgeff and Filippi (1957) is described. Although it has been used successfully to repeat the crosses by Burgeff and Filippi, the technique was developed for making crosses with *S. kraussiana* and its varieties, and the following description is based on work with these taxa. Application of this technique to a study of inheritance of pigmentation in *S. kraussiana* var. *aurea* W. Bull will be the subject of a later report.

DESCRIPTION OF THE TECHNIQUE

Plants were grown in flats or pots in the greenhouse. Under natural daylengths, abundant spores were produced from spring through fall, but spore production was much diminished during the winter. Supplemental light from 6PM to 6AM was provided by three 110 w, incandescent bulbs suspended 50 cm above the plants; this was found to increase the period of spore production.

Strobili of *S. kraussiana* and its varieties typically bear a single basal megasporangium; the remainder of the strobilus is microsporangiate. The ripe megasporangia protrude noticeably from the strobilus, and can be removed with a pair of fine forceps. The excised megasporangia are placed in a petri dish where, upon drying, they dehisce, shedding their spores. The megaspores are collected and stored in vials. At room temperature, stored megaspores remain viable for several months. According to Robert (1971), megaspores of *S. kraussiana* exhibit 90%

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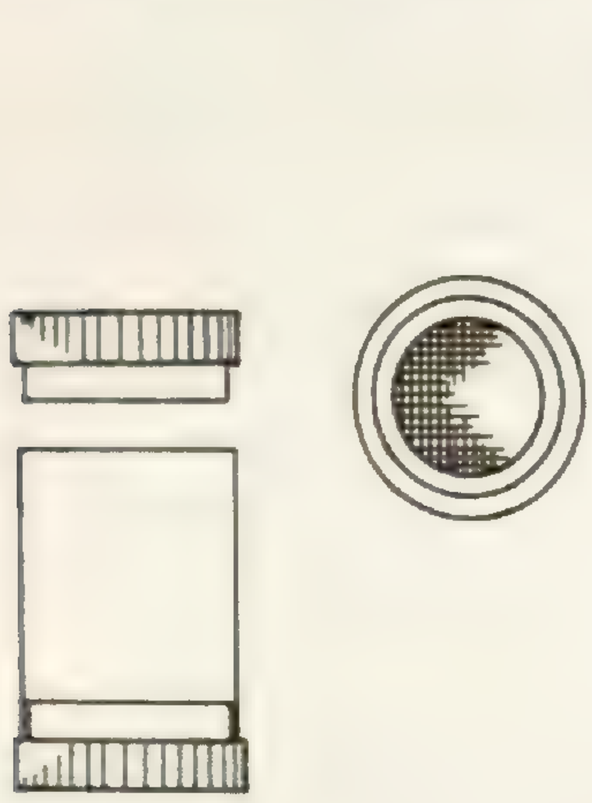
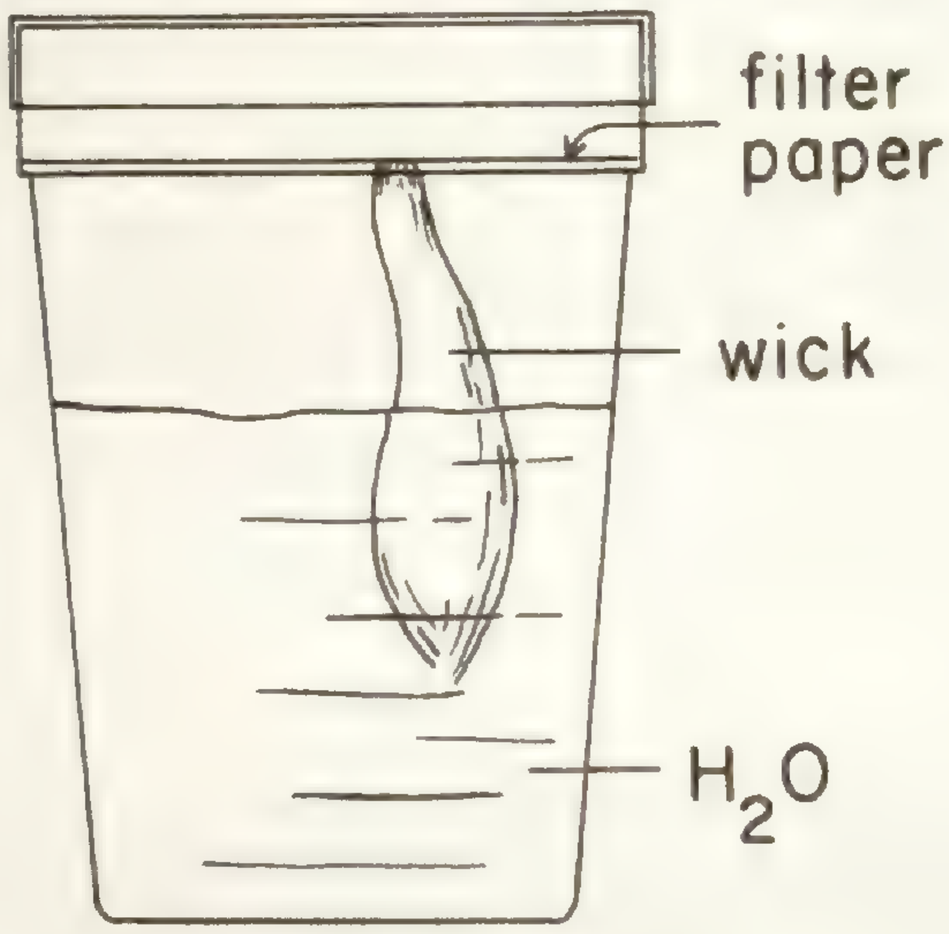
germination if cultured immediately following harvest and less than 50% if culture is delayed for three months. A detailed study of viability of stored megaspores of *Selaginella* is needed.

Megaspores of *S. kraussiana* and its varieties exhibit a prominent reticulate sculpturing. Microspores possess long spines and tend to adhere to the sculptured surface of megaspores. Any adhering microspores can be removed by washing the megaspores thoroughly prior to incubation. The washing apparatus developed for this purpose consists of a short length of plastic tubing fitted at each end with a polyethylene stopper modified to hold a fine nylon screen cloth (*Fig. 1*). Tygon





1 2

FIG. 1. Apparatus (side and end views) for washing megaspores and microsporangia. FIG. 2. Self-watering incubation device.

tubing 1.5 cm in diameter and 2.0–2.5 cm long was found convenient. The stoppers used were those supplied with Kimble Opticlear vials, size 19 × 48 mm. The bottom of each stopper was cut off, and a rod was inserted into the hollow interior to push out the top insert. The center of the insert was cut out, leaving a thin ring. Nylon screen cloth with a mesh opening of 240 μm was laid over the top of the stopper and secured by snapping the ring back into place. The washing apparatus containing megaspores is immersed in a container through which there is a stream of running water. A 30–40 minute rinse is sufficient to remove any adhering microspores and to pass them through the mesh, leaving only clean megaspores inside. Megaspores of *S. kraussiana* measure 800–1500 μm in diameter (Robert, 1971), and microspores 50–70 μm (Robert, 1973), thus the reason for using a 240 μm mesh opening in the washing apparatus.

After washing, megaspores are removed and incubated on layers of filter paper in a self-watering device (*Fig. 2*). The device consists of a 100 ml polypropylene beaker, on top of which rests a plastic petri dish with a hole drilled in the bottom. One end of a cotton wick is inserted into the hole with the opposite end in contact with distilled water in the beaker. The layers of filter paper in contact with the wick remain constantly moist. A similar device was used by Robert (1971) to germinate megaspores of *S. kraussiana*.

Unlike megasporangia, microsporangia do not protrude from the strobilus at maturity and must be selected with the aid of a dissecting microscope. In dissections of strobili, mature microsporangia can be detected by their amber color and granular texture. Typically a mature strobilus bears one or two ripe microsporangia. Since intact microsporangia containing microspores are incubated, dehiscence of microsporangia must be prevented. Therefore, the dissection is carried out on wet filter paper. The microsporangia are then washed using the same procedure as described for the megaspores, and are then sown on filter paper kept moist by the self-watering device described above. Separate cultures are maintained for microgametophytes and megagametophytes.

The author maintains cultures in a growth chamber at a temperature of 21 ± 2°C and a light intensity of 125 ft-c obtained with fluorescent illumination. A 12-hr light/12 hr dark cycle is used. Under these conditions, megaspores germinate in 8–14 days, and the resulting megagametophytes can be maintained for several months with no exogenous nutrients. The endogenous food reserve, composed of lipid and protein (Robert, 1971), is sufficient to support the slow-growing megagametophytes. Although some gametophytes may become contaminated, infection by microorganisms is usually minimal, so that an occasional change of filter paper and water is sufficient for maintaining the gametophytes.

For fertilization experiments, the author uses megagametophytes which are several weeks old. Such gametophytes possess numerous archegonia and tufts of rhizoids. Microsporangia incubated for 4–12 weeks contain mature microgametophytes. Microsporangia cultured for longer than 12 weeks often contain microspores which have already shed their contents. To obtain swimming spermatozoids, 5–10 microsporangia are placed in the cavity of a depression slide containing a drop of distilled water. The sporangia are teased apart with fine dissecting tools, thus dispersing their endosporic microgametophytes. Within a few minutes, spermatocytes are released. A short time later, each spermatocyte releases a single biflagellate spermatozoid which swims away rapidly. Slagg (1932) and Robert (1973, 1974) have described the details of microgametophyte and spermatozoid development in *S. kraussiana*. Since each microspore contains approximately 250 spermatocytes and each sporangium contains approximately 600 microspores (Slagg, 1932), large numbers of sperm are contained in a single water droplet. The shedding of sperm can be hastened by chilling the microsporangia prior to teasing them open. The chilling can be accomplished by placing the depression slide containing the sporangia in a refrigerator (7°C) for 4–6 minutes.

Two methods have been used to achieve fertilization. The megagametophytes may be placed directly in the drop of water containing sperm. Upon microscopic examination, a dramatic chemotactic response can be seen as the male gametes are attracted to the archegonial pad. After several minutes, a dense aggregation of spermatozoids is visible in the vicinity of the archegonia. As previously noted by Slagg (1932), the spermatozoids are active for approximately 30 minutes.

Another method for achieving fertilization is to transfer the layers of filter paper containing megagametophytes from the self-watering device to a petri dish. The

sperm-containing droplet is then added to the megagametophytes. To ensure adequate moisture for the swimming spermatozoids, additional water is added. Since some microgametophytes may not release their gametes immediately, the megagametophytes are left in the sperm bath overnight. Fertilization treatments may be repeated at weekly intervals. In experiments with *S. kraussiana* and its varieties, two or three treatments resulted in 60–90% successful fertilizations. After the fertilization procedure, the megagametophytes are again incubated on filter paper in the self-watering device. To check for the possible occurrence of apogamy, some unfertilized megagametophytes are incubated separately as controls. Repeated tests have shown no evidence for apogamy in *S. kraussiana* and its varieties.

Sporelings appear in fertilized cultures 4–6 weeks after fertilization. Sporelings will grow for several weeks on filter paper moistened with distilled water, the endogenous food reserve of the megagametophyte serving to nourish the young sporophyte.

Eventually the sporelings can be transferred from filter paper to soil in a pot. Fine forceps should be used to avoid damaging the delicate roots. The soil mixture used by the author consists of a finely sifted sandy loam. To prevent dislodging the delicate sporelings, the soil is watered by setting the pot in a tray of water. To maintain the sporelings in a moist atmosphere, the surface of the pot is covered with plastic or glass. The pots are maintained in the growth chamber until the sporelings are firmly established, after which the pots are transferred to the greenhouse. Each sporeling eventually develops into a mat of intertwined stems which form at their tips spore-bearing strobili. For *S. kraussiana* and its varieties, the time required to complete the life cycle, from spore to spore, is 9–11 months.

Crossing techniques have been widely used for homosporous pteridophytes (Lovis, 1968). Through their use, much has been learned about the genetics and breeding systems of ferns (Klekowski, 1971). However, with the exception of the study by Burgeff and Filippi (1957), the heterosporous genus *Selaginella* has been neglected in this regard. It is hoped that the method described here will encourage further work into the genetics and breeding systems of *Selaginella*.

The author wishes to thank Mr. James A. Tanno for his helpful suggestions and Ms. Virge Kask for preparing the illustrations.

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A Tropical Fern Grotto in Broward County, Florida

DANIEL F. AUSTIN,* GRACE BLANCHARD IVERSON,** and CLIFTON E. NAUMAN*

John K. Small (1931, p. 1) once wrote that Florida should be known as the "land of ferns." Several areas throughout the state have become famous for their abundance of these plants. Most notable are the rocklands of Dade County (Small, 1920a, b), the Pineola Grotto of Citrus County (Harper, 1916; Lakela, 1964), and the lakes region of Central Florida (Small, 1932, p. 15; Wherry, 1964, p. 28; Lakela & Long, 1976, e. g., p. 123). No one has even suspected until recently (Nauman, 1978) that Broward County boasted ferneries. Few even believe that a site remains unreported that contains the most impressive display of ferns in the southern end of the state.

The site we hereby record is located in Sects. 5,6, T49S, R42E (*Fig. 1*) and contains almost half of the pteridophyte species known in tropical Florida. Furthermore, it appears to have the largest and healthiest populations in the state of some of the rarer species. We call the site the "Cypress Creek Hammock" because it represents a remnant of the Cypress Creek drainage system (Steinberg, 1976). Vegetation in the area is complex, with swamp forest, hammocks, pinelands, and fallow fields.

A limestone outcrop of undetermined affinity (J. E. Hoffmeister, 1978, pers. comm.) forms a ridge on the western limit and islands near the eastern side. This broken ridge system was dissected by Cypress Creek before the area was drained by canals, and the central swamp is overlain with various depths of peat and sand.

We have been studying the site since September 1976. During that time, we have discovered that it contains over 200 species of plants, and the list grows with each visit. Not only is the site the last remaining stronghold of ferns in southeastern Florida, but it contains range extensions for several plants (e.g. *Asplenium trichomanes-dentatum, Catopsis floribunda, Polypodium ptilodon, Tectaria heracleifolia, Tectaria incisa, Tillandsia valenzuelana),* and several species on the Smithsonian and Florida Committee Rare and Endangered Plant lists (e.g. *Asplenium trichomanes-dentatum, Asplenium serratum, Epidendrum nocturnum, Ophioglossum palmatum, Tillandisa flexuosa).*

Cypress Creek Hammock is unique in several ways: in its number of ferns, for its range extensions, and for existing as an "island" of native vegetation in metropolitan Broward County. We believe that any one of these factors makes the site worthy of preservation, and that their combination makes it imperative. Some of our colleagues have been helpful toward this end by writing letters. We solicit letters or support in other ways from all those interested in ferns, plants, and native Florida habitats.

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We have received help and encouragement from many individuals in our study. In particular, we wish to thank the following: G. N. Avery (Everglades National Park), E. S. Ayensu (Smithsonian Institution), D. S. Correll and Helen Correll (Fairchild Tropical Garden), R. A. DeFillips (Smithsonian Institution), A. M. Evans (University of Tennessee), J. Greis (formerly Broward Co. forester), D. Lellinger (Smithsonian Institution), J. Popenoe (Fairchild Tropical Garden), A. R. Smith (University of California, Berkeley), and R. G. Stolze (Field Museum, Chicago).

FERNS OF CYPRESS CREEK HAMMOCK

Acrostichum danaeifolium Langsd. & Fisch. (Pteridaceae). Leather Fern. Frequent in swampy areas.

Anemia adiantifolia (L.) Swartz (Schizaeaceae). Pine Fern. Occasional colonies in pineland areas on the fringe of the hammock and swamp.

Asplenium trichomanes-dentatum L. (Aspleniaceae). Spleenwort. Several small colonies following a limestone outcrop along the swamp/hammock interface; rare.

Asplenium serratum L. (Aspleniaceae). Bird's-nest Fern. Several plants in leaf litter and at bases of hammock trees; rare.

Blechnum serrulatum L. C. Rich. (Blechnaceae). Swamp Fern. Common throughout the swamp.

Campyloneurum phyllitidis (L.) Presl (Polypodiaceae). Strap Fern. Abundant as an epiphyte on fallen logs.

Ctenitis sloanei (Poepp.) Morton (Aspidiaceae). Florida Tree Fern. At least six colonies occur: one contains 20 adults with fronds exceeding 1 m and more than 30 sporelings. This is probably the largest population of this species in the United States.

Ctenitis submarginalis (Langsd. & Fisch.) Copel. (Aspidiaceae). Brown-hair Comb Fern. This species is reported as new for Broward County, having been found there since Nauman (1978) was in press. Several plants; rare.

Nephrolepis biserrata (Swartz) Schott (Davalliaceae). Giant Sword Fern. Abundant in various parts of the hammock.

Nephrolepis exaltata (L.) Schott (Davalliaceae). Sword Fern. Common throughout.

Ophioglossum palmatum L. (Ophioglossaceae). Hand Fern. Rare in Florida, yet the site contains at least 30 individuals.

Osmunda regalis var. *spectabilis* (Willd.) A. Gray (Osmundaceae). Royal Fern. Occasional in the swamp.

Phlebodium aureum (L.) J. Smith (Polypodiaceae). Cabbage Palm Fern. Common wherever cabbage palms grow.

Polypodium polypodioides var. *michauxianum* Weath. (Polypodiaceae). Resurrection Fern. Common, especially on oaks.

Polypodium ptilodon var. *caespitosum* (Jenm.) Evans (Polypodiaceae). Plume Polypody. Rare epiphytes; the plants are smaller than the more typical size in other parts of their range.

Psilotum nudum (L.) Pal. Beauv. (Psilotaceae). Whisk-fern. Common; mostly on the bases of cabbage palms.

Pteridium aquilinum var. *latiusculum* (Desv.) Underw. (Pteridaceae). Bracken. Infrequent in shaded areas.

Pteris tripartita Swartz (Pteridaceae). Giant Brake. Occasional in disturbed parts of the swamp.

Pteris vittata L. (Pteridaceae). Chinese Brake. Occasional along paths and other disturbed parts of the hammock; usually on rocks.

Salvinia minima Baker (= *S. rotundifolia auctt. non* Willd.) (Salviniaceae). Water Fern. Occasional in ponds in the swamp.

Tectaria heracleifolia (Willd.) Underw. (Aspidiaceae). Halberd Fern. Occasional but local on limestone outcrops.

Tectaria incisa Cav. f. *incisa* (Aspidiaceae). At least two colonies are known from this location. Known elsewhere from a few sites in Dade County (Nauman, 1978).

Thelypteris dentata (Forsk.) E. St. John (Aspidiaceae). Occasional in disturbed parts of the hammock.

Thelypteris interrupta (Willd.) Iwatsuki (= *T. totta* (Thunb.) Schlepe) (Aspidiaceae). Common in the swamp.

Thelypteris kunthii (Desv.) Morton (= *T. normalis* (C. Chr.) Moxley) (Aspidiaceae). Marsh Fern. Frequent in the hammock.

Thelypteris ovata R. St. John var. *ovata* (Aspidiaceae). Occasional on limestone outcrops.

Thelypteris reptans (Gmel.) Morton (Aspidiaceae). Creeping Fern. One small colony known.

Thelypteris torresiana (Gaud.) Alston (= *Macrothelypteris torresiana* (Gaud.) Proctor) (Aspidiaceae). Occasional in disturbed parts of the hammock.

Vittaria lineata (L.) J. E. Smith (Vittariaceae). Shoestring Fern. Frequent on cabbage palms.

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REVIEW

"EVOLUTIONARY PATTERNS AND PROCESSES IN FERNS," by J. D. Lovis in R. D. Preston and H. W. Woolhouse (eds.). Advances in Botanical Research, vol. 4, pp. 229–415. 1977. Academic Press, London and New York. ISSN 0-12-005904-5. $30.00.—Professor Lovis has written a tour de force that is the most important summary of evolutionary mechanisms in ferns since Professor Manton's seminal book on fern cytology published over 25 years ago. Lovis' paper begins with a detailed consideration of the fossil record and how it relates to the classification and phylogeny of recent ferns. A careful list of chromosome numbers in fern genera is given. A classification of living ferns by family and subfamily is proposed that takes both fossil and chromosome data into full account. Polyploidy is discussed at length and is analyzed by its systematic and geographic distribution. Present knowledge of genome analysis, cytogenetics, introgression, breeding systems, and apomixis in ferns is all summarized. An extensive list of references concludes the work. Unfortunately, they are cited without article titles, and so are of limited use apart from their mention in the text.—*D.B.L.*

Studies of the Azolla–Anabaena Symbiosis Using Azolla mexicana, I. Growth in Nature and Laboratory

ROBERT W. HOLST[1] and JOHN H. YOPP*

The symbiosis of *Azolla* and *Anabaena* is the only known association of a pterophyte with a cyanophyte. *Anabaena azollae* is found in all species of the aquatic heterosporous fern *Azolla*. It is enclosed within a small, basal cavity of the upper green lobe of the bilobed, alternate leaves. Very rapid propagation of the intact *Azolla* is generally achieved by fragmentation, but may occur by germination of algal-infected sporocarps (Rao, 1935; Smith, 1955, pp. 371–383). In many temperate and tropical regions, *Azolla* is considered a pest because it can cover a farm pond or rice paddy rapidly (Sculthorpe, 1967). However, it has long been cultivated as a green manure for rice crops in southeast Asia (Moore, 1969). This latter use provides the basis for the recent intense interest in this unique symbiosis. The algal symbiont is a nitrogen-fixing organism that behaves much like *Rhizobium* species do in their symbioses with legumes.

Studies on the factors affecting the growth of the *Azolla–Anabaena* symbiosis are relevant to research on nitrogen-fixation and also weed control. Previous laboratory studies on nitrogen-fixation have employed *A. filiculoides* Lam. or *A. caroliniana* Willd. (Ahmad, 1941; Peters & Mayne, 1974). However, of the six New World species, *A. mexicana* Presl is the major representative of the central and western United States (Svenson, 1944). The present study was conducted to characterize the optimal environment for growth of *A. mexicana*. By virtue of environmental preferences or a more controllable or rapid growth rate, this species might provide a better and more convenient model than larger land plants do for studies of symbiotic nitrogen fixation.

MATERIALS AND METHODS

Studies in the natural environment.—Growth of *Azolla mexicana* was studied in a small, 2 ha pond in southwestern Jackson County, Illinois. This pond, in the Mississippi River flood plain, is fed by runoff from low alluvial plains and swamps delimited by levees.

The environmental factors recorded at each observation were light intensity (Weston photometer), light quality (IL 150 Photometer, International Light, Newburyport, MA.), photoperiod, air temperature in the shade and in the sun, and water pH and surface and bottom temperature. Total plant cover of the pond surface and the percentage contributed by *A. mexicana* were also recorded. Plant cover was determined by the line intercept method from photographs of the pond surface (Canfield, 1941).

Laboratory studies. — Plant material was collected from the pond on 18 June 1975. It was separated and washed clean of other aquatic plants. All subsequent

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experiments were performed with material vegetatively reproduced from this collection.

Several media successfully employed for culture of aquatic plants (including *Azolla* spp.) were tested singly and in various combinations for their capability to support the growth of *A. mexicana* (Johnson et al., 1966; Olsen, 1970; Lahdesmaki, 1968; Ahmad, 1941; Nickell, 1958; Peters & Mayne, 1974). Buffers were not used unless specifically noted in the tables or figures. The pH was adjusted with either N KOH or HC1.

Plants were maintained in deep, rectangular, polyethylene containers partially covered with plate glass to obtain a humidity higher than ambient. The number of initial plants per container was approximately one per 10 cm^2. Culture density was selected from preliminary experiments, which indicated that crowding is an important variable.

The containers were placed in walk-in growth chambers (Sherer-Gilette Model CEL 511-38) that were set for different light intensities, photoperiods, and day/night temperatures.

All growth studies were conducted using 5 plants per replicate. Each set of five plants was grown in a 125 ml Erlenmeyer flask containing 50 ml of culture medium.

Growth is expressed as a fold change which was determined from the formula: fold change = Wt/Wo, where Wt is fresh weight at time of sampling and Wo is initial fresh weight of the culture. A fold change of 2 indicates doubling in fresh weight. The number of days or hours to attain this value is designated the doubling time.

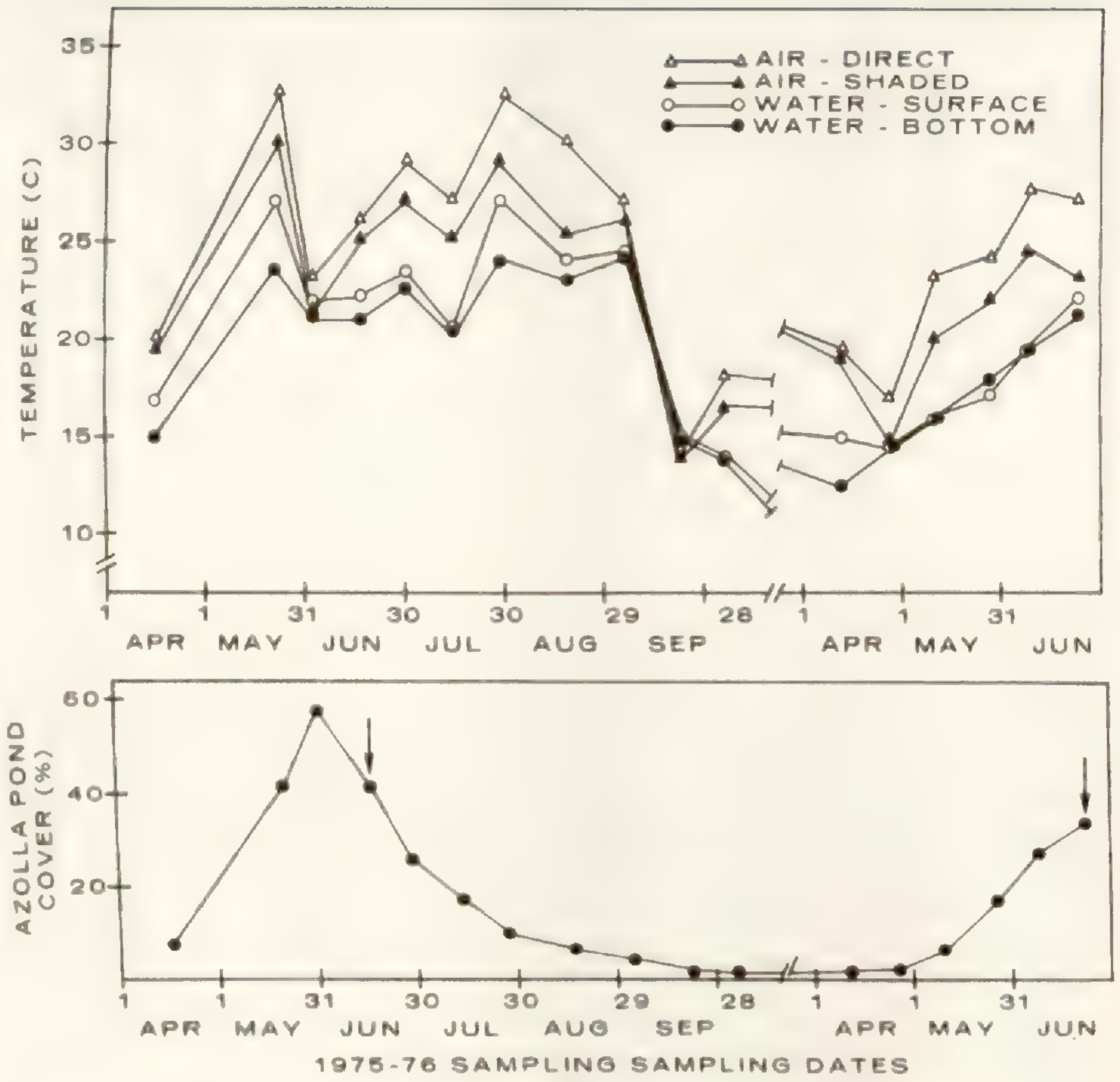
Chlorophyll content was determined by the measurement (Beckman DBGT spectrophotometer) of the optical density (O.D.) at 652 nm of an 80% acetone extract of a plant homogenate. The method of Arnon (1949) was used in the following form:

$$\frac{\text{O.D.}_{652\text{nm}}}{3.45} \times \frac{\text{ml of liquid}}{\text{g FW}} = \text{mg chlorophyll/g FW}$$

All experiments were replicated three times. Means, standard variations, and F test probability were determined using multiple regression analysis (Kelley et al., 1969). Student's t-test and correlations were obtained using the IBM 5100 Basic Statistic Program.

RESULTS AND DISCUSSION

Natural environment study.—The appearance of *A. mexicana* in its natural habitat was strongly correlated with surface and bottom temperatures of the pond *(Fig. 1)*. The critical temperature (approximately 15° C) was attained early in April of 1975, but not until after 1 May 1976 due to cooler and fluctuating temperatures, which delayed the appearance of the fern. Light intensity and, of course, photoperiod were not greatly different for the two spring seasons. Numerous observations indicated that floating sporophytes resulted from the temperature-dependent germination of zygotes in the bottom mud.



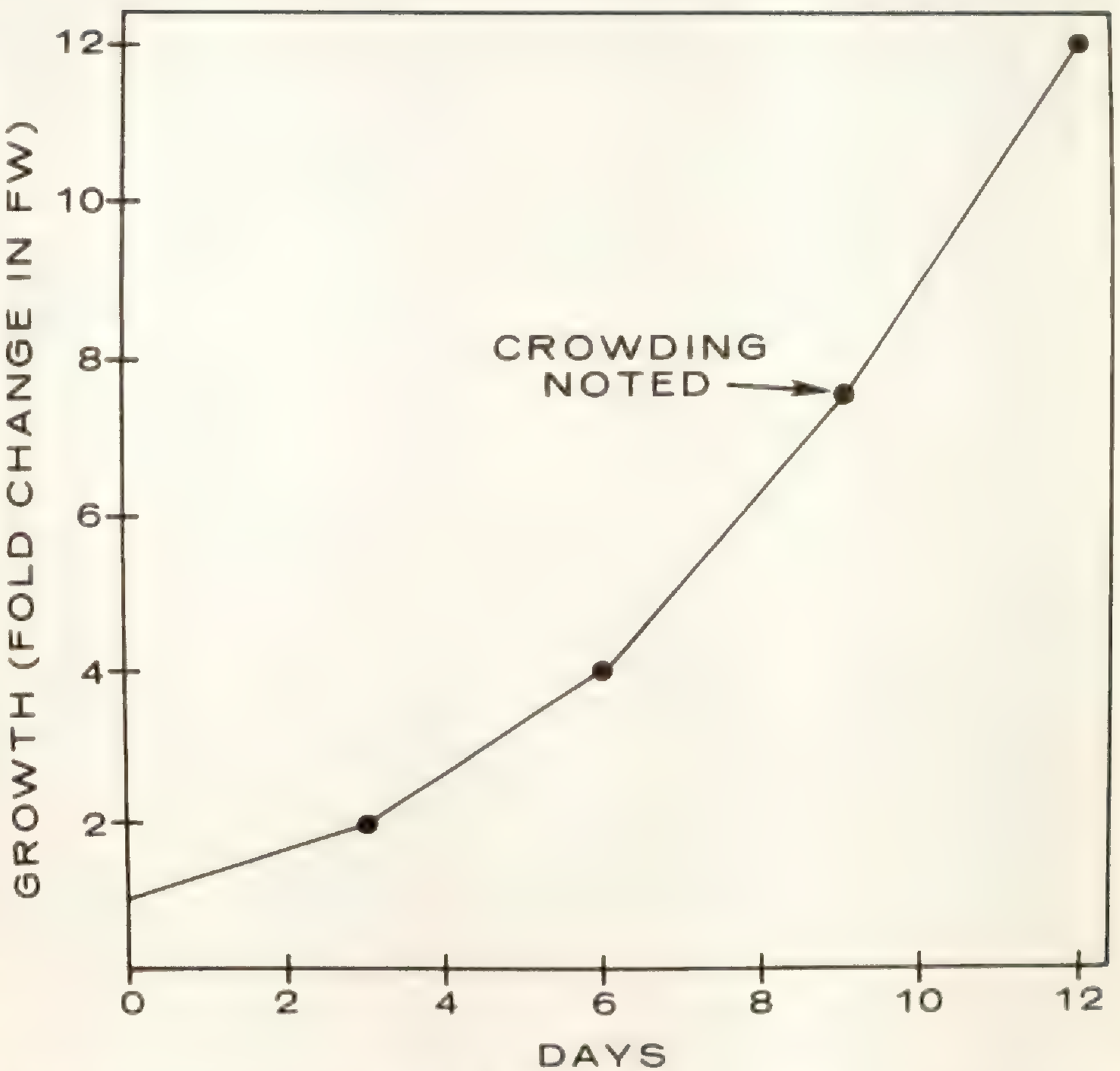


FIG. 1. Relationship of total pond cover by *A. mexicana* with surface and bottom temperatures of the pond. Arrows denote time of observed sporulation. FIG. 2. Growth curve of an *A. mexicana* culture in the basic medium in a 10 hr., 18°C night and 14 hr, 23°C day (13 klux light intensity) regime.

The earlier and more extensive vegetative growth of the fern during the spring of 1975, as compared to that of the following spring, also paralleled the much more rapid rise and higher water temperatures attained in 1975. After the water temperatures rose to 20° C, *A. mexicana* became the dominant, floating, emergent plant in the study location. The total plant cover was almost 60%, with the fern accounting for 80–90% of that total.

The fern showed signs of increasing red pigmentation and senescence in the open areas of the pond. Light intensity there was 95 to 120 klux (*Table 1*), and temperatures remained fairly constant from May through August of 1975. Photoperiod was apparently not a factor because *A. mexicana* was seen to increase in May and June of 1976, a period of decline in 1975. The green plants along the shaded shoreline accounted for the fern's presence in the summer months, even when water temperatures exceeded 25°C. The light intensity never exceeded 3 klux in these shaded areas. High light intensity, therefore, appears to be the factor most responsible for senescence of this fern. Ahmad (1941) gave a similar explanation for senescence of *A. pinnata* R. Br. Light quality did not significantly change throughout the study period (*Table 1*).

TABLE 1. TOTAL ILLUMINATION (klux) AND SPECTRAL INTENSITIES ($\mu w/cm^2 \cdot nm$) OF LIGHT ON CLOUDLESS DAYS AT 10 AM LOCAL TIME, SUMMER 1975, AT BRUSHY BAYOU POND.

Area	*Total light*	*Red light*	*Far red light*	*Blue light*
Direct sun	95–120	110–125	90–100	15–115
Shade	3–0	5–7	6–9	5–12

Sexual reproduction, as shown by mega- and microsporocarp production, occurred in both years of the study in June (*Fig. 1*, arrows). Since the populations were decreasing in June 1975 and increasing in June 1976, photoperiod may be the principal trigger of sporulation.

A second growth of *A. mexicana* was noted in fall of 1974, when water temperatures remained between 18 and 25°C. However, September 1975 was very cool, water temperatures fell below 15°C, and *A. mexicana* did not reappear.

During its season, the fern grew well in the shaded areas of the pond and even on the moist bank. There was, however, an apparent correlation between soil moisture and the survival of the *A. mexicana*, even on obviously moist soil. There was a relatively distinct level in the moist soil bank above which the fern was not found.

The pH of the pond ranged from 6.3 through 6.8 throughout the study.

Previous studies on other species of *Azolla* indicate that the intact fern grows well under reduced light conditions, at a pH of 5 to 7, and at temperatures not exceeding 23 to 25°C (Ahmad, 1941; Moore, 1969; Olsen, 1970). *Azolla mexicana* appears to have similar environmental requirements.

Laboratory studies.—Preliminary experiments based on the natural environmental study showed that a photoperiod of 14 hours light/10 hours dark, a 12 klux light intensity (cool white fluorescent), and a 23°C day/18°C night thermoperiod were optimal for growth. These values were employed in laboratory experiments

unless otherwise noted. Temperature, pH, light intensity, osmotic stress, nutrient element concentration and salinity were the experimental variables in the laboratory studies.

Growth medium.—Although *A. mexicana* grew on all the media tested, a medium was devised by extensive experimentation that gave superior results (*Table 2*). The doubling rate in this medium was 68 to 75 hours if other conditions were optimal. This is about 48 hours less than that reported by Nickell (1958) for *A. mexicana* and for *A. caroliniana* (Dr. Gerald Peters, pers. comm.). It is similar to that reported for *A. pinnata* (Brotonegoro & Abulkadir, 1976).

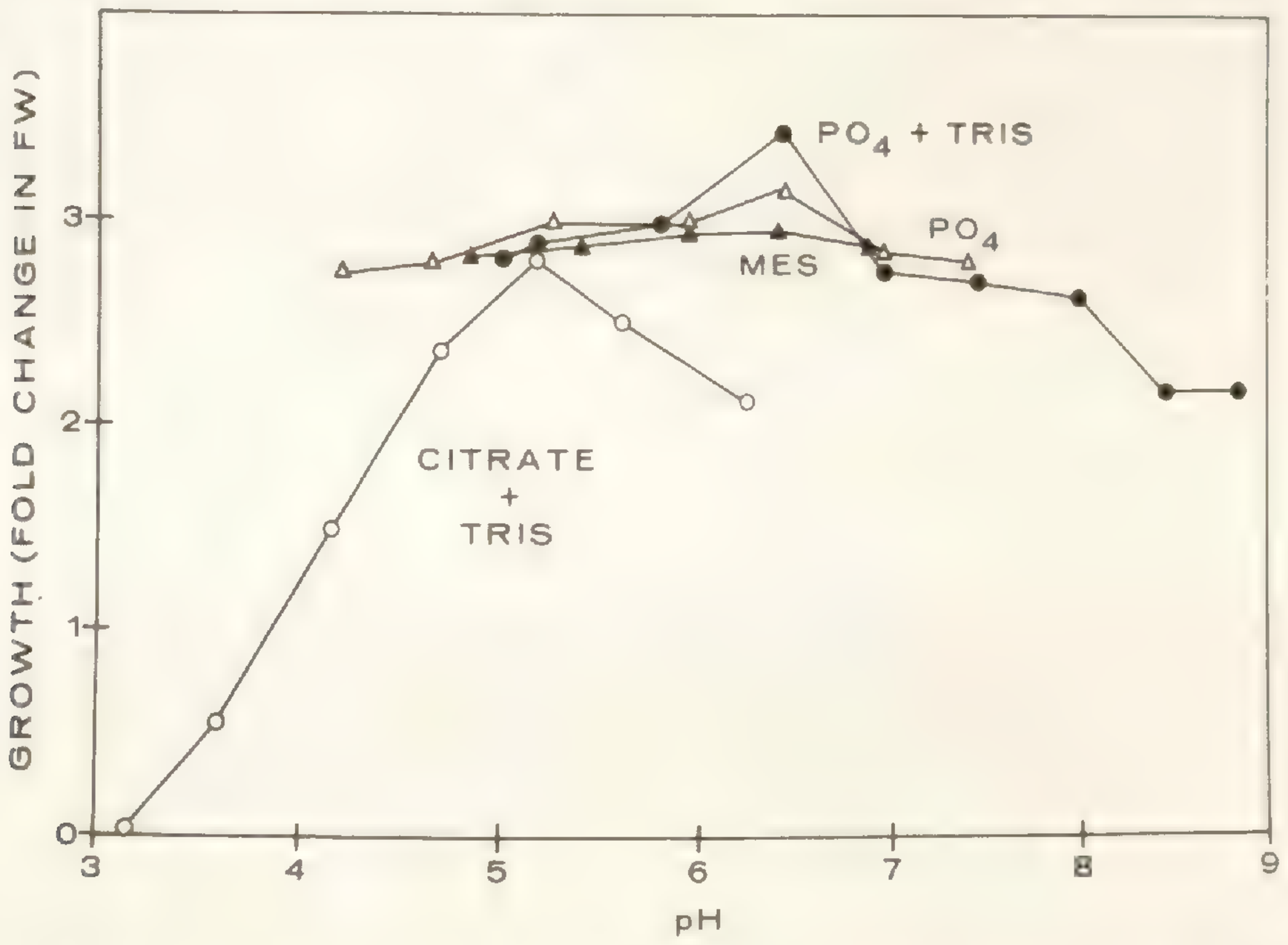


FIG. 3. Effect of pH on *A. mexicana* growth under environmental conditions as in *Fig. 2*. Buffers (10 mM) were PO_4 (potassium phosphate), citrate (citric acid–sodium citrate), TRIS (Tris [Hydroxy methyl]-amino methane), and MES (2-[N-Morpholina] ethane sulphonic acid).

Crowding effect.—A typical growth curve for *A. mexicana* obtained under optimal conditions is given in *Fig. 2*. The culture generally reached its most rapid growth rate after five days. The rapid rate continued for up to 12 days and if crowding was noted, decreased rapidly thereafter. Crowding was scored when overlapping of fronds between plants occurred. Mats of ferns up to 2 cm thick frequently were observed. Cultures could be thinned and the remaining plants fragmented by hand without experiencing a reduction in growth. Similar mat formation and results from fragmentation have been reported for *A. filiculoides* in African waters (Ashton & Walmsley, 1976).

pH of medium.—The pH of the unbuffered medium was set at 6.5. However, after two to three days the pH dropped to 4.2 and remained constant thereafter. If the medium was not changed biweekly, *A. mexicana* began to produce yellow-edged fronds. A variety of buffers (phosphate, Tris, MES, citrate) were used at 0.5 mM to determine accurately the pH range of *A. mexicana*. It grew well over the pH range of 4.2–8.0 (*Fig. 3*). Below pH 4.2, growth decreased dramatically.

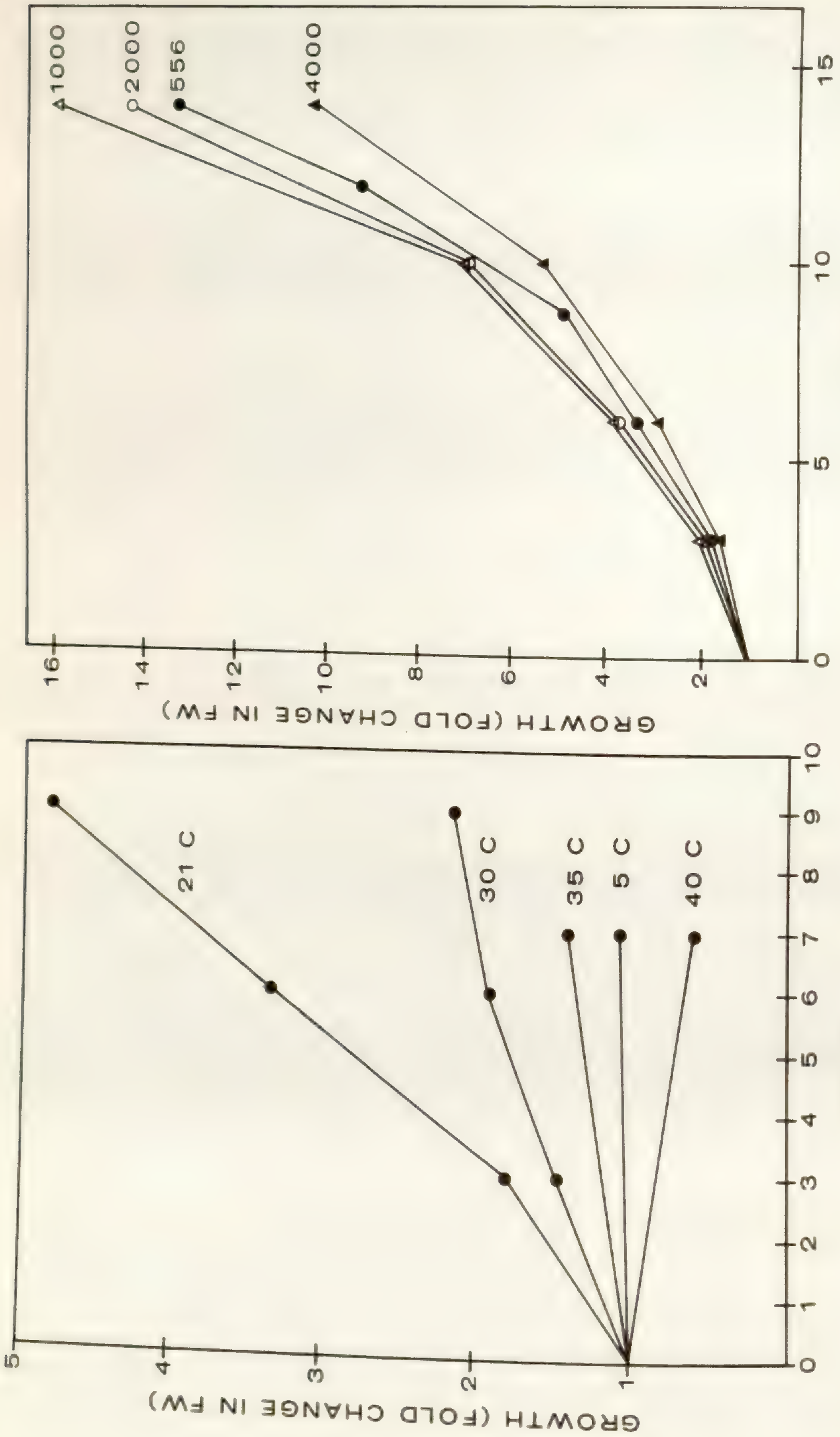


FIG. 4. Effect of temperature on *A. mexicana* growth. Significant differences between treatments are indicated by * ($P=0.01$). All other environmental conditions as in *Fig.* 2. FIG. 5. Effect of salinity (NaCl) on *A. mexicana* growth. Values represent ppm NaCl content of the medium. The basic medium contains 556 ppm. All other environmental conditions as in *Fig.* 2.

The peak noted at 6.5 was not significant (P=0.01). The decline in growth above 5.1 with citrate and Tris buffers may be due to the buffers *per se*. Other buffers used were not toxic above 5.2. This optimal pH range agrees with that reported by Nickell (1958) for *A. mexicana* and for other species of the fern (Moore, 1969; Olsen, 1970). Ashton and Walmsley (1976), however, reported dual, light intensity-dependent pH optima. This was not observed in the present study.

Temperature effects.—When *A. mexicana* was cultured under low light intensities (less than 13 klux), it grew well at temperatures up to 30°C (*Fig. 4*). Growth slowed at 35°C and the fern died within seven days at 40°C. Growth ceased but the plants remained green and viable at 5°C.

A similar temperature range and optimum were reported for *A. pinnata* in Asia by Moore (1969). *Azolla filiculoides* in Africa has a higher temperature optimum (27.5°C) and a broader range (5 to 45°C), according to Ashton and Walmsley (1976). The same species in India possesses a temperature range and optimum similar to that of *A. mexicana* (Ahmad, 1941).

TABLE 2. BASIC MEDIUM FOR MAXIMUM GROWTH OF INTACT *Azolla mexicana* IN VITRO.

Macronutrients	*mg/l*	*Micronutrient stock*[1]	
$CaCl_2 \cdot H_2O$	176	H_3BO_3	286 mg
KH_2PO_4	53	$CoCl_2 \cdot 6H_2O$	5 mg
KCl	78	$MnCl_2 \cdot 4H_2O$	181 mg
$MgSO_4 \cdot 7H_2O$	240	$ZnSO_4 \cdot 7H_2O$	22 mg
Fe stock[1]		$CuSO_4 \cdot 5H_2O$	8 mg
FeChel[2]	250 mg	$NaMoO_4 \cdot 2H_2O$	13 mg
$FeSO_4 \cdot 7H_2O$	250 mg	NaCl	100 mg
H_2O	50 ml	H_2O	100 ml

[1] Use 1 ml/l of medium.
[2] FeChel is sodium ferric diethylenetriamine penta-acetate–Sequestrene 330 Fe Iron Chelate (10% metallic Fe) sold by Ciba-Geigy.

Solute tolerance.—Addition of NaCl to produce a salt concentration of 2000 ppm in the medium had no significant effect on growth (*Fig. 5*). At 4000 ppm solutes, growth was slightly reduced. Over the range of 556 (basal medium) to 4000 ppm solutes, only a slight decrease in chlorophyll was observed (700 to 500 μg chlorophyll/g FW).

The review by Moore (1969) indicated that *Azolla* species were killed after three weeks in Knop's solution (1500 ppm salts). Haller et al. (1974) found that *A. caroliniana* grew well in a sea and pond water mixture of 3000 ppm solute and was not killed by a salt content of 16,000 ppm.

Osmotic effects.—In order to separate the effect of the salts themselves from the osmotic effect they exert, *A. mexicana* was grown in media of varying polyethylene glycol (PEG) content. The failure of the fern to grow on moist mud in the natural environment suggested inhibition due to low water potential. Since growth occurred in 4000 ppm NaCl, which is equivalent to -1.69 bars (Nobel, 1974), a range of 0 to -10 bars was selected. As seen in *Fig. 6*, growth steadily decreased down to -5 bars. There was no growth below -5 bars, but the fern

remained green and viable. The effect of lowered water potential due to PEG parallels that due to salt, indicating more of an osmotic than an ionic effect produced by salts.

Light intensity.—Light intensity was a major growth regulator. At intensities above 20 klux, orange-red pigmentation developed rapidly. Within seven days, plants ceased growth and entered into a senescent phase. Growth did not occur below 0.75 klux

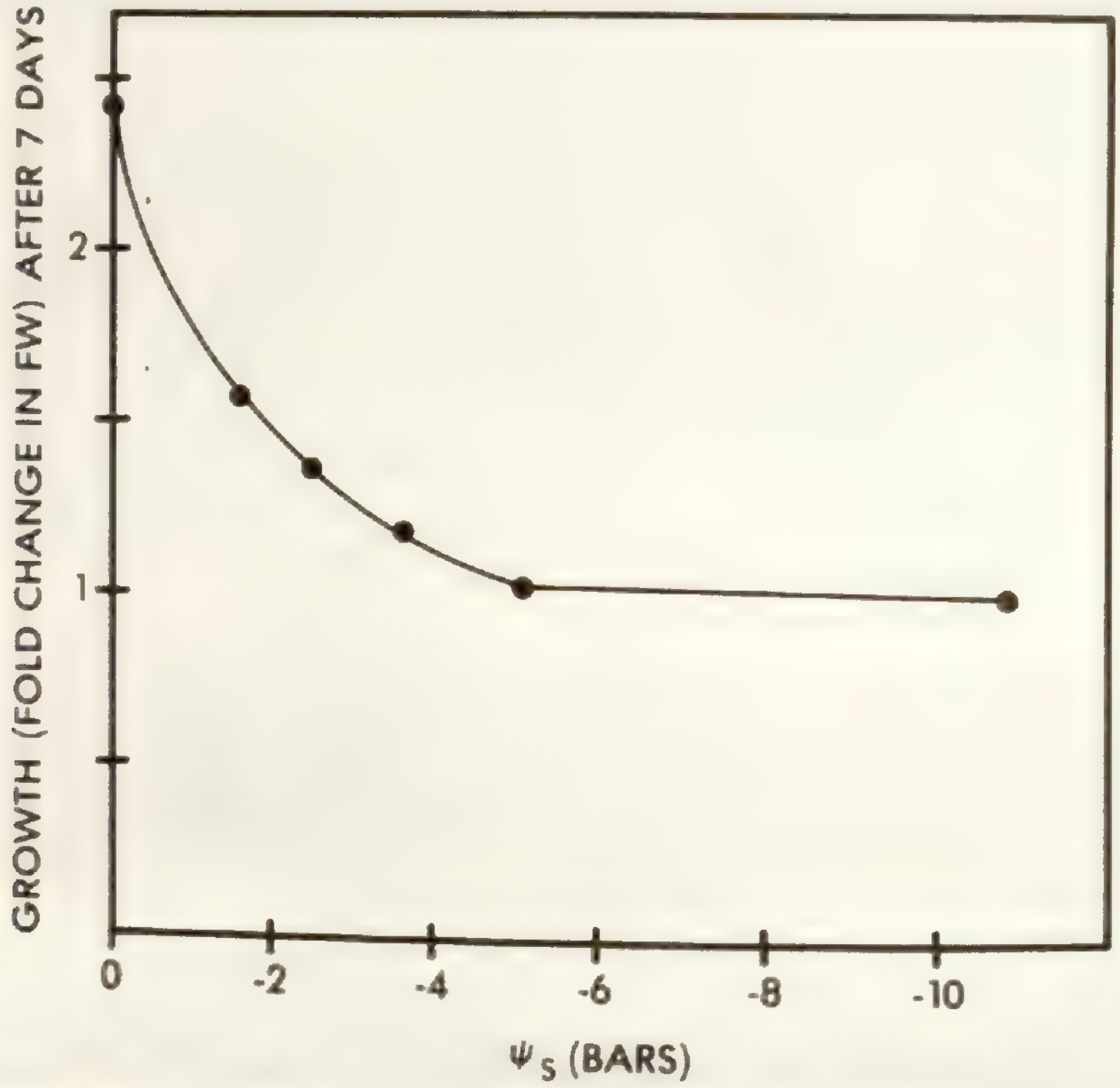


FIG. 6. Effect of osmotic stress on *A. mexicana* growth. The values are for seven days' growth in media containing appropriate amounts of polyethylene glycol (PEG 6000). All other environmental conditions as in *Fig. 2.*

The present study has revealed the major environmental variables affecting the growth of *A. mexicana.* These data and the formulation of a growth medium that supports one of the most rapid growth rates reported for a species of *Azolla* will enable *A. mexicana* to be used as an experimental organism.

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Thelypteris in Arkansas

W. CARL TAYLOR* and DAVID M. JOHNSON**

Recent herbarium studies and field work indicate that the genus *Thelypteris* in Arkansas is represented by four species. Two of these, *T. kunthii* (Desv.) Morton and *T. torresiana* (Gaud.) Alston, are reported here for the first time in the state.

In the United States, *T. kunthii*, a neotropical species, is found in open or partially shaded, moist depressions on the coastal plain from South Carolina to Texas (Smith, 1971). Specimens of *T. kunthii* have been collected from Lee and Pulaski Counties (central and east central Arkansas), but both collections were made from plants persisting in garden plots. These plants do not appear to have escaped cultivation sufficiently to be considered naturalized. However, numerous plants recently have been found in Ashley County (southeast Arkansas) which are scattered over several square miles of cut-over pine-hardwood forest northwest of the town of Crossett (*Fig. 1*). These plants undoubtedly are naturalized and probably became established as a result of new habitats created by lumbering operations in the area. Common associated species in these open, disturbed habitats include *Rhus copallina, Liquidambar styraciflua, Callicarpa americana, Quercus stellata, Acer rubrum, Diospyros virginiana, Berchemia scandens, Pteridium aquilinum* var. *pseudocaudatum, Onoclea sensibilis, Polystichum acrostichoides*, and *Asplenium platyneuron* var. *incisum*.

Thelypteris torresiana, a species native to Asia, was first discovered in the United States in 1904. An interesting historical account of its collections is given by Leonard (1972), who also postulates the occurrence of this species in southeastern Arkansas. The discovery of *T. torresiana* in virtually the same area of Ashley County and in habitats like those of *T. kunthii* suggests that disturbance from lumbering is also responsible for the establishment of *T. torresiana* (*Fig. 2*). The discovery of naturalized plants of *T. kunthii* and *T. torresiana* extends the known range of both these species north into the coastal plain of southeastern Arkansas (*Fig. 6*).

Thelypteris noveboracensis (L.) Nieuwl., which in Arkansas inhabits moist, rocky soils of woods and thickets along streams, reaches the southwestern extent of its range in the Ouachita Mountains (*Fig. 3*). The known Arkansas populations of *T. noveboracensis* are over 200 miles from the nearest reported stations in the Ozark Hills of southern Illinois and the Tennessee River Hills of northeastern Mississippi.

Populations of *T. palustris* Schott are found scattered around the state in low, marshy areas near springs, ponds, and lakes, and along streams (*Fig. 4* and *5*). Two varieties of *T. palustris* have been reported for Arkansas (Demaree, 1943). Although most Arkansas material is clearly referrable to var. *pubescens* (Laws.) Fern., var. *haleana* Fern. has been reported in Drew and Bradley Counties. These two populations also contain var. *pubescens* and forms that appear to be transitional between the two varieties.

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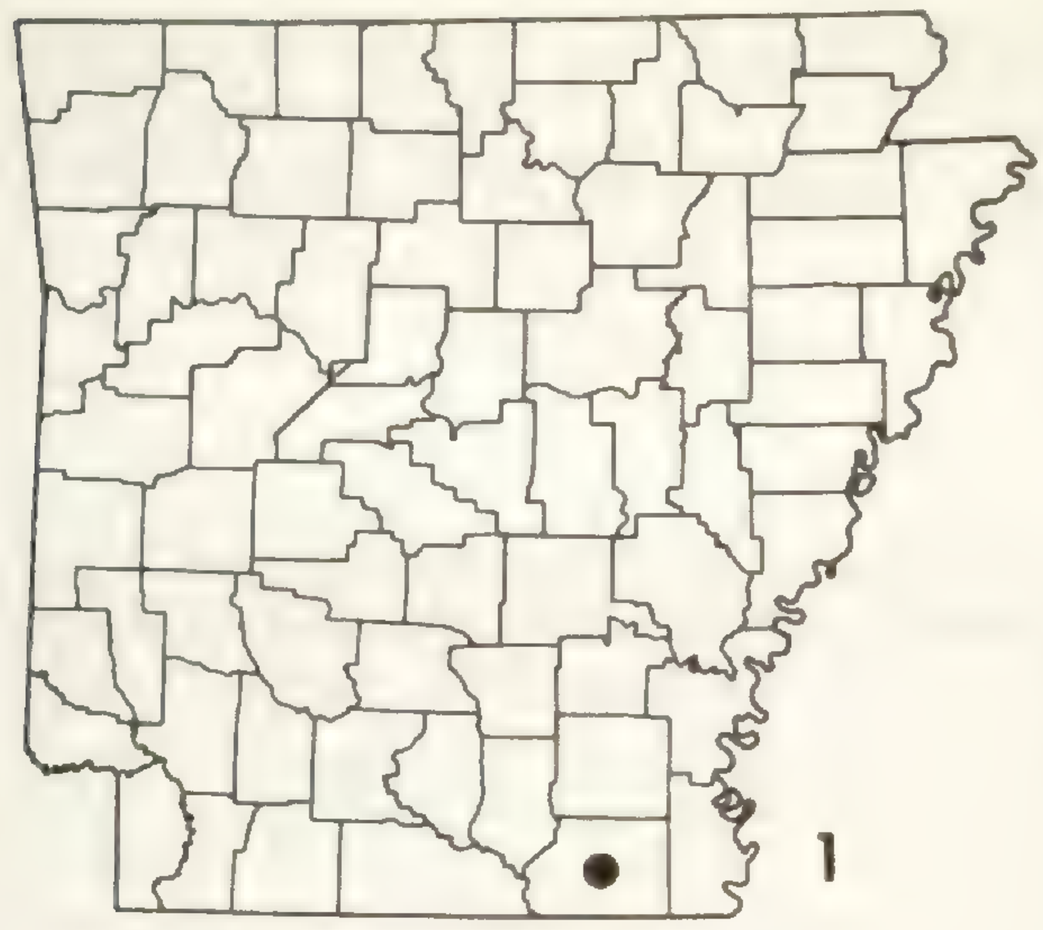
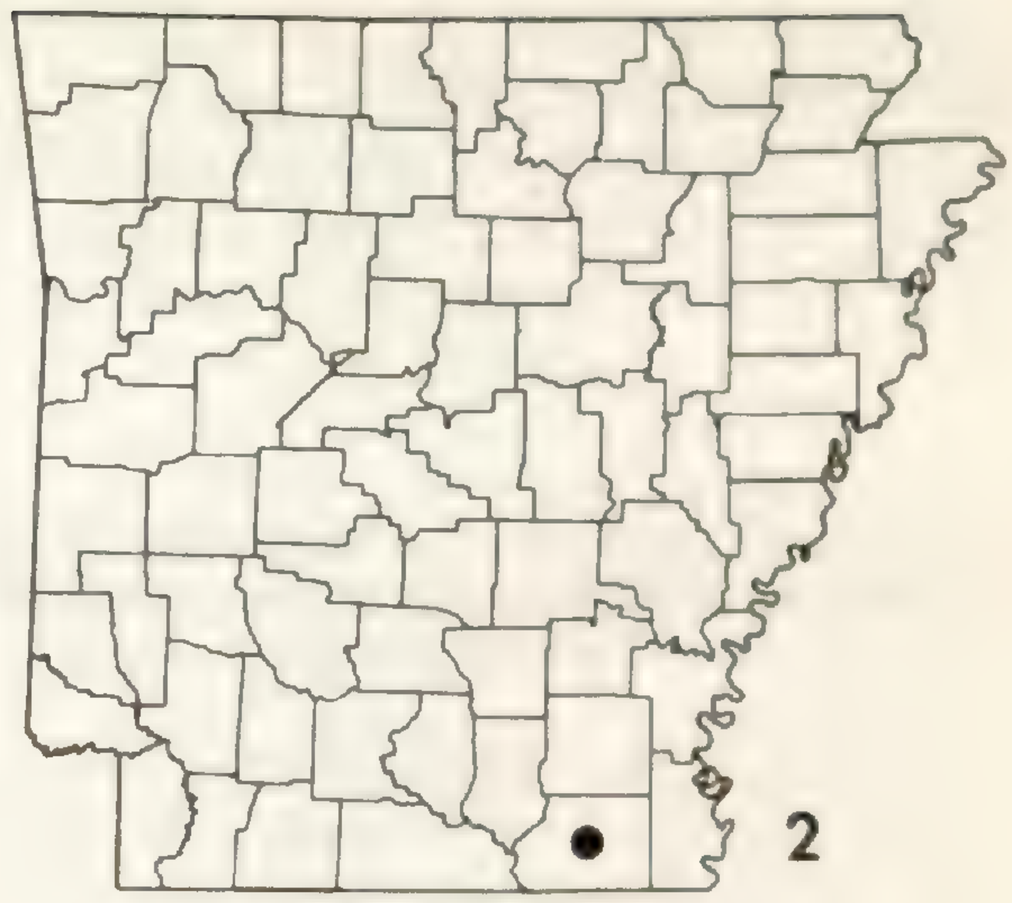


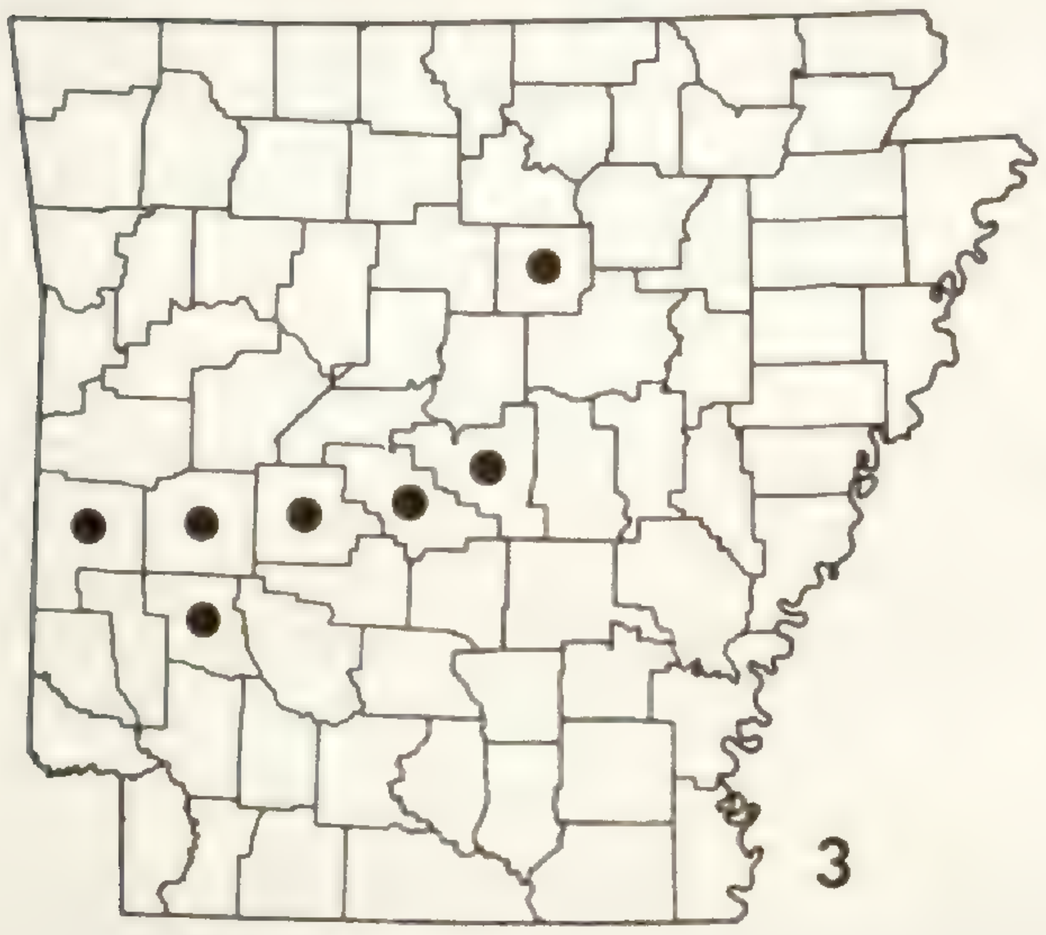
1

Thelypteris kunthii



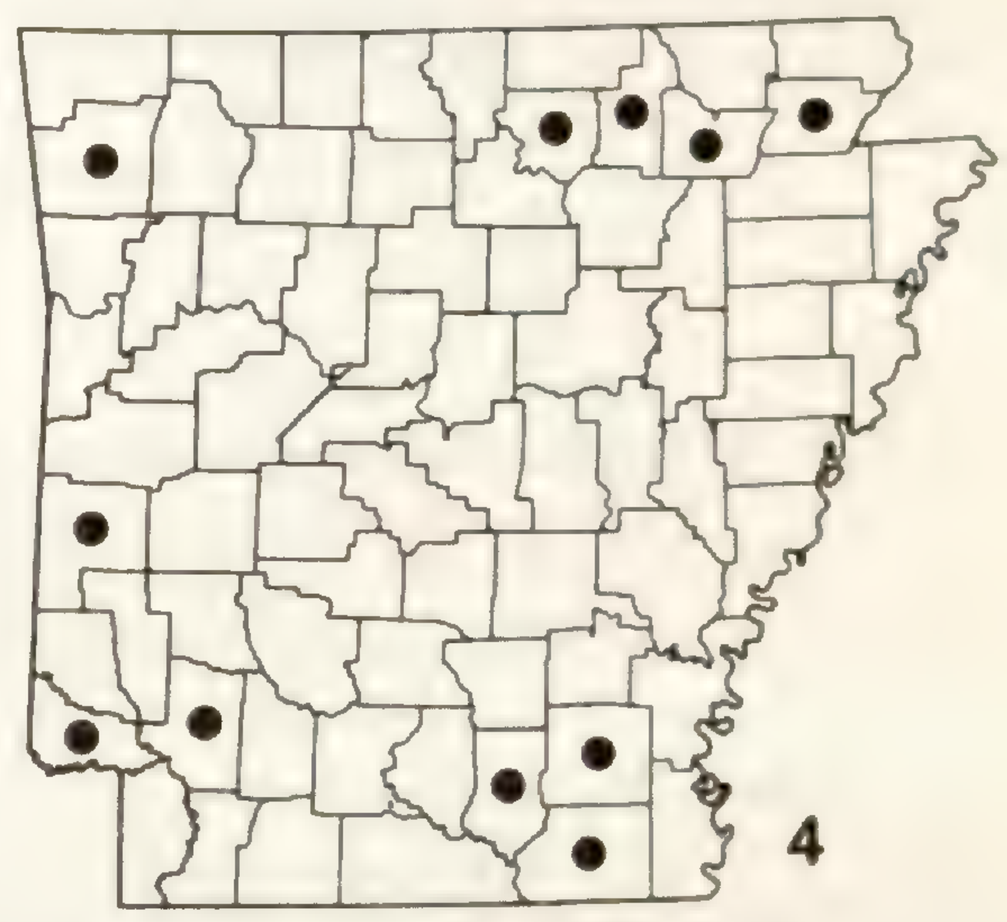
2

Thelypteris torresiana



3

Thelypteris noveboracensis

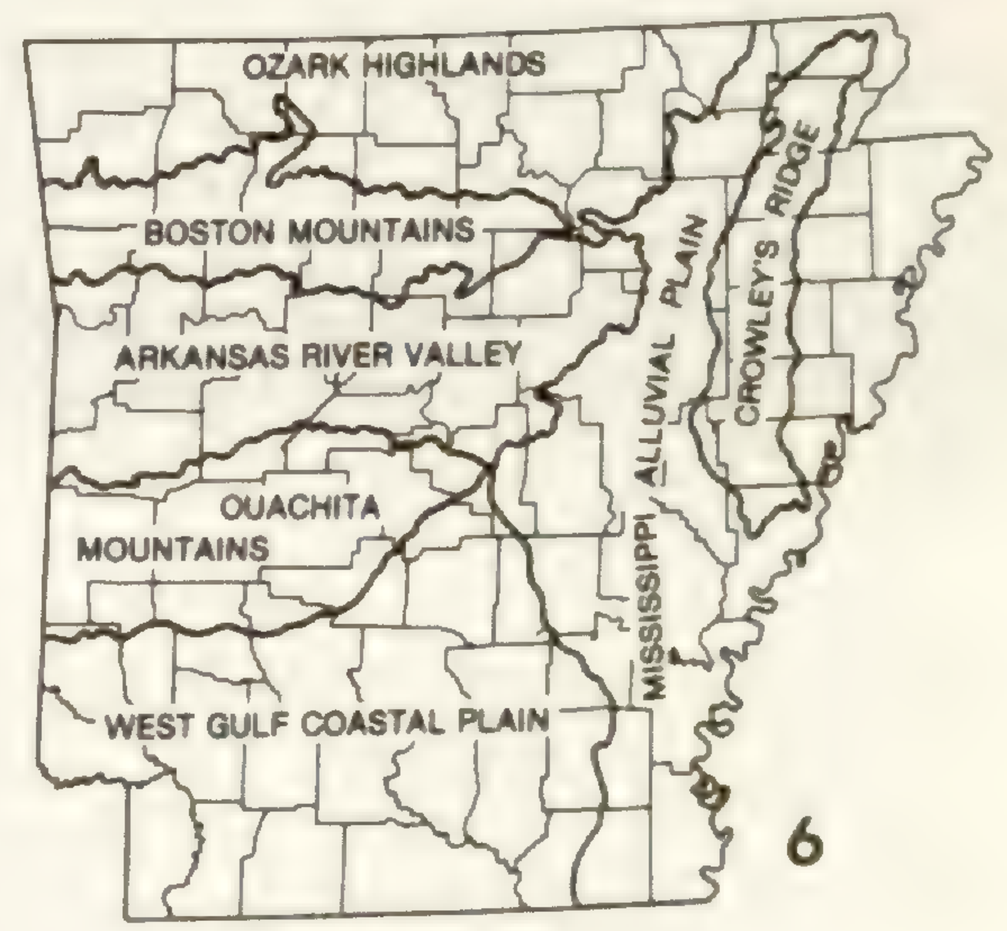


4

Thelypteris palustris
var. *pubescens*

5

Thelypteris palustris
var. *haleana*



6

FIGS. 1-5. Distribution maps of Arkansas *Thelypteris*. FIG. 6. Physiographic regions in Arkansas.

We wish to thank Dr. Alan R. Smith for checking the identifications of *T. kunthii* and *T. torresiana*.

REPRESENTATIVE COLLECTIONS:

Thelypteris kunthii: **Ashley Co.:** Along timber access road SE of Lake Georgia-Pacific; T17S, R9W, sect. 35, 25 Oct 1975, *Johnson 281* (Hendrix College).

Thelypteris torresiana: **Ashley Co.:** Along timber across road W of Crossett; T18S, R9W, sect. 9, 25 Oct 1975, *Johnson 283* (Hendrix College).

Thelypteris noveboracensis: **Cleburne Co.:** *Johnson 393* (Hendrix College). **Garland Co.:** *Moore 6278* (APCR). **Montgomery Co.:** *Taylor 1084* (SIU). **Pike Co.:** *Taylor 2903* (SIU). **Polk Co.:** *Moore 410261*. (UARK). **Pulaski Co.:** *Johnson 112* (Hendrix College). **Saline Co:** *Moore 480154* (UARK).

Thelypteris palustris var. *pubescens:* **Ashley Co.:** *Johnson 276* (Hendrix College). **Bradley Co.:** *Demaree 19445* (MO). **Drew Co.:** *Moore 420048* (UARK). **Greene Co.:** *Moore 480685* (UARK). **Hempstead Co.:** *Moore 480353* (UARK). **Izard Co.:** *Johnson 422* (Hendrix College). **Lawrence Co.:** *Taylor 1794* (SIU). **Little River Co.:** *Palmer 8359* (MO). **Polk Co.:** *Moore & McWilliam s.n.* (UARK). **Sharp Co.:** *Wade 167* (UARK). **Washington Co.:** *Henbest 16* (UARK).

Thelypteris palustris var. *haleana*: **Bradley Co.:** Cypress swamp near Warren, *Demaree 19445* (SMU). **Drew Co.:** Swamp near Wilmar, *Demaree 24624* (SMU).

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ROBERT J. RODIN (1922–1978)

Robert Joseph Rodin was born in Sacramento, California, on 15 July 1922. He lived in Eureka and in Turlock in his youth. During World War II service in the U.S. Marine Corps, he was stationed in Guam and China. In 1948 he married Elva Bain, who, with three daughters, survives him. He received a Ph.D. degree in botany from the University of California at Berkeley in 1951. After graduation, he accepted a position as a professor of biology at Forman Christian College, Lahore, West Pakistan. He collected ferns in the Himalayas extensively during this time. From 1953 until his retirement in 1976, Rodin was a professor of biology at California Polytechnic University in San Luis Obispo. His research specialties included the anatomy of the Gnetales, ethnobotany of Ovamboland, and the taxonomy of the pteridophytes of California, an interest which led to his publishing the "Ferns of the Sierra" for the Yosemite Natural History Association. In recent years he was active in the conservation movement in California. In 1966–67 he was a Fulbright Professor at the University of Delhi. He also took part in botanical expeditions to South Africa in 1947 and to southwestern Africa in 1973. He died in San Luis Obispo on 27 June 1978.—*D.B.L.*

SHORTER NOTES

VITTARIA LINEATA REDISCOVERED IN GEORGIA. — *Vittaria lineata* (L.) J. E. Smith, the Shoestring Fern, is primarily restricted to peninsular Florida reaching as far north as Citrus Co. on the Gulf coast and Duval Co. on the Atlantic coast (E. T. Wherry, The Southern Fern Guide, Doubleday, 1964). However, a disjunct population had been known since 1938 in Lincoln Co., Georgia. This piedmont population grew in pits in south-facing sandstone cliffs. Unfortunately, this area was quarried and the original locality destroyed. Thus, as far as known, *Vittaria* has been extinct in Georgia for some years.

This note reports the rediscovery of *V. lineata* in Georgia on Cumberland Island, Camden Co. The plants were observed at three localities on the island some distance apart. Two sites were bark fissures of Live Oak trees (*Quercus virginiana* Miller); the third was in a bark fissure of Sweet Bay (*Magnolia virginiana* L.) All sites were approximately one meter above the ground on the east and southeast exposures of the tree boles. One specimen (*Worthington 336*) is on deposit at the University of Georgia herbarium, and another (*Stoneburner s.n.*, 19 Sept 1978) is in cultivation at the University of Georgia Plant Growth Facilities.—*James G. Bruce, Department of Botany,* and *D. L. Stoneburner, James I. Richardson,* and *Joanne Worthington, Institute of Ecology, University of Georgia, Athens, GA 30602.*

THE DISTRIBUTION OF DRYOPTERIS GOLDIANA AND D. MARGINALIS IN MISSOURI. — *Dryopteris goldiana* (Hooker) Gray is one of the rarest ferns in Missouri. The only known occurrences have been early collections made in two isolated locations along the eastern border of the state. These were noted by Steyermark in "Flora of Missouri" (1963, p. 40). In July, 1976, I discovered the first locality for this species on the western side of the state. Plants were found growing in rich loess deposits underlain by local limestone formations in a ravine tributary to an unnamed intermittent drainage north of the Missouri River in south-central Clay County, in a city park within the city limits of Kansas City. This particular site is 200 miles from either of the two previously recorded Missouri locations, and suggests that perhaps *D. goldiana* also occurs in the interior sections of Missouri, although it has not been recorded from there. Habitat information listed in Gleason and Cronquist's "Manual of Vascular Plants of Northeastern United States and Adjacent Canada" (1963, p. 24) noted a preference for moist woods in circumneutral soil. The Kansas City site is Knox Silt Loam soil, pH 5.6–7.3. Other fern species found in association with *D. goldiana* show the richness of the site: *Adiantum pedatum* var. *pedatum*, *Athyrium pycnocarpon*, *Botrychium virginianum*, *Cystopteris fragilis*, *Dryopteris marginalis*, *Onoclea sensibilis*, and *Woodsia obtusa*, as well as liverworts. The richness of the fern flora at this site is unique in northwestern Missouri.

The presence of *Dryopteris marginalis* (L.) Gray at this site is unusual, for this species is commonly found in shaded crevices of rock ledges and bluff sites in

Missouri where soils are generally derived from sandstone, chert, or granite. While in the same vicinity of *D. goldiana*, the plants of *D. marginalis* were found at a slightly higher elevation on a north-facing slope. *Dryopteris marginalis* also was located on the thick loess deposit, an unusual substrate for this species in Missouri. This particular location is the northwesternmost occurrence of *D. marginalis* in Missouri; Steyermark's "Flora of Missouri" (1963, p. 40) recorded it from Saline County, 75 miles east of this latest discovery. The species is fairly common south of the Missouri River in most counties of the Ozarks, but has not been found in the northwestern part of the state.

The site was nominated as one of Missouri's State Natural Areas, representing the rich river hills community type as well as preserving the habitat for a rare Missouri species, *D. goldiana*. Through a cooperative agreement between the Kansas City Parks Department and the Missouri Department of Conservation, State Natural Area status was approved in February 1978.

Documentary specimens have been filed in the herbaria of the University of Missouri at Columbia (UMO) and at Kansas City. — *Greg F. Iffrig, Missouri Cooperative Wildlife Research Unit, Stephens Hall, University of Missouri, Columbia, MO 65211.*

GYMNOGRAMMA VS. GYMNOGRAMME. — Confusion has existed over the proper spelling and gender of the generic name *Gymnogramma*. Although this name is illegitimate (see Underwood, Bull. Torrey Bot. Club 29:617-634. 1902), its wide use in the past has made it often quoted in current literature. The name has been considered to be either feminine or neuter and has been alternatively spelled *Gymnogramme*.

In originally naming the genus *Gymnogramma*, Desvaux (Berl. Mag. 5:304. 1811) cited the derivation of gramma as from the Greek meaning "line." In this sense, the word gramma (*γραμμά*) is the Doric form of the more usual Attic Greek gramme (*γραμμή*) (Pichi-Sermolli, Webbia 21:487-505. 1966). Both words have the same meaning and both are feminine in gender. The problem arises from the similar-looking Attic Greek word, gramma (*γράμμα*), which is neuter and means "that which is drawn" or "letter." Some authors, unaware of the feminine Doric form gramma and/or confused by the identical spelling of the different neuter Attic word gramma, have decided that Desvaux's use of gramma as feminine was improper and that the word should either be considered as neuter or should be changed to gramme. However, since Desvaux specified that gramma means "line," and treated it as feminine, he clearly was intentionally and correctly employing the Doric form of gramme. Modifications of the generic name to *Gymnogramme* or specific epithets to a neuter ending are not correct.

This clarification has a rather wide application since there are names of many fern genera based on gramma or gramme (e.g. *Anogramma, Coniogramme*, etc.). In all cases when these are derived from the Greek word meaning "a line," the original spelling, whether as gramme or gramma, should be maintained and epithets should have a feminine termination. If there are any derived from the

Greek word meaning "that which is drawn" or "a letter," these also should retain their original spelling but with epithets of a neuter termination. Where a derivation is not included, gender of the name should follow that published with the name.—*Christopher H. Haufler* and *Rolla M. Tryon, Gray Herbarium, Harvard University, 22 Divinity Avenue, Cambridge, MA 02138.*

REVIEW

"FERNS," by Philip Perl and the Editors of TIME-LIFE Books, Alexandria, Va. 1977. 159 pp. + many photographs; numerous watercolors by Richard Crist. $8.95.—To say that this volume is beautifully illustrated and contains a wealth of information for the amateur fern grower is true, but it also is an oversimplification that does not do justice to the term "review." In fact, this book is a good example of a modern, mass-produced encyclopedia volume. It is an attractively packaged hodge-podge of enticing tidbits of information which are priceless for beginning fern growers. Unfortunately, the editors were too intent on interjecting poetic and artistic touches, rather than on fulfilling their implied purpose of giving comprehensive information on fern growing, including recent and advanced knowledge of the subject.

The introductory chapter is a delightfully written historical sketch, but is broken up by the inappropriate interposition of photographic essays having little or no relationship to the text. The remaining chapters fare a bit better in this regard. There is much to be gleaned from the horticultural information in chapter four, although I doubt that many readers will find a ready supply of builder's sand. Perlite, which is available nearly everywhere and which is included in most soil preparations based on the Cornell mix, is omitted here, although many of the cultural suggestions in chapter five include it.

The photographic illustrations are superb, especially those in the essay on identifying ferns by family. On the other hand, I found the delicately attractive watercolors in chapter five to be little more than decorative. They have an ethereal quality not always representative of the stark greens and bold forms of the species they pretend to illustrate. For example, the excellent photographs of the Hacksaw fern on pages 70 and 72 bear little resemblance to the illustration on page 110. A number of the watercolors appear so similar as to be of little value in distinguishing between superficially similar but distinct genera.

The fern encyclopedia comprising chapter five is the meat of the volume, and occupies the second half of the book. It contains some identifying characteristics of a variety of ferns, mostly cultivated, their provenance, and hints on their culture, with recommended temperature, foot-candles of light, and pH readings ad infinitum, as if the latter two were all that important. I am not convinced that the average fern grower will ever determine his foot candles or pH, or even care. Elsewhere in this work the ubiquitous Asparagus-fern is defrocked, but in chapter five, *Selaginella* and *Equisetum* are treated as if they were legitimate ferns. An extensive and useful bibliography is given on pages 152–153.

Considered as a whole, even with its idiosyncracies, this is a handy and attractively priced volume for fern growers.—*Robert Read, Department of Botany, Smithsonian Institution, Washington, DC 20560.*

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A Community of Lycopodium Gametophytes in Michigan

JAMES G. BRUCE* and JOSEPH M. BEITEL**

Since Fankhauser's discovery of *Lycopodium annotinum* gametophytes in 1873, the sexual plants of *Lycopodium* have been sought repeatedly, and yet they remained elusive. There are now only 27 species for which gametophytes (19 subterranean, 8 surficial) have been found, representing fewer than 7% of the species.

The continuing rarity of gametophytes cannot be attributed to a lack of searchers in temperate areas, although since most club-mosses are tropical it does point in part to the geographical separation between most botanists and most species of *Lycopodium*. But the gametophytes of even such common temperate species as *L. tristachyum*, *L. digitatum*, *L. appressum*, as well as those of the less common North American plants such as *L. porophilum* an *L. prostratum*, either never have been described or have been described so poorly as to render discussion almost meaningless. This lack of knowledge is due partly to the infrequent occurrence of the gametophytes and further to the fact that the more frequently encountered temperate species have subterranean gametophytes. Detection of the latter is dependent upon finding attached emergent sporophytes (*Fig. 2*). That they can be found and sometimes even in great numbers is amply illustrated by Spessard (1922) and Eames (1942).

In this paper we report finding a community of nearly 500 gametophytes in a Jack Pine plantation in Michigan representing five (or possibly six) species of *Lycopodium: L. annotinum*, *L. clavatum*, *L. digitatum*, *L. lucidulum*, and *L. obscurum*. *Lycopodium dendroideum* also may be present but is apparently indistinguishable gametophytically from *L. obscurum*. A key to these species is given below. *Lycopodium digitatum* has not been reported from nature previously (Wilce, 1965; Bruce, 1976) and its naturally occurring gametophytes are described here for the first time. Whittier (1977) has reported gametophytes of this species from culture.

KEY TO THE GAMETOPHYTES AND/OR YOUNG SPOROPHYTES OF LYCOPODIUM SPECIES

1. Paraphyses (multicellular uniseriate sterile hairs around the sex organs) present: thallus generally axial or branched axial ..... *L. lucidulum*
1. Paraphyses absent; thallus usually not axial, but if axial, then tapering and carrot-shaped.
   2. Gametophytes carrot-shaped ..... *L. digitatum*
   2. Gametophytes disc-shaped, sometimes with convoluted edges, occasionally nearly spherical.
      3. Leaves of young sporophytes with long, bristle tips ..... *L. clavatum*
      3. Leaves of young sporophytes merely acuminate.
         4. Leaves of young sporophytes more than 7 mm long; gametophytes highly convoluted and fragile ..... *L. annotinum*
         4. Leaves of young sporophytes less than 5 mm long; gametophytes coarsely convoluted and sturdy ..... *L. obscurum/dendroideum*

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FIGS. 1–3. Habitat and habit of gametophytes and young sporophytes of *Lycopodium*. FIG. 1. Jack Pine plantation with opening occupied by several Black Cherry trees. FIG. 2. Young emergent sporophyte of *L. obscurum*, ca. ×1. FIG. 3. Young sporophyte and gametophyte (white tuberous structure embedded in sandy soil at end of sporophytic stem) of *L. lucidulum*. ×1.5.

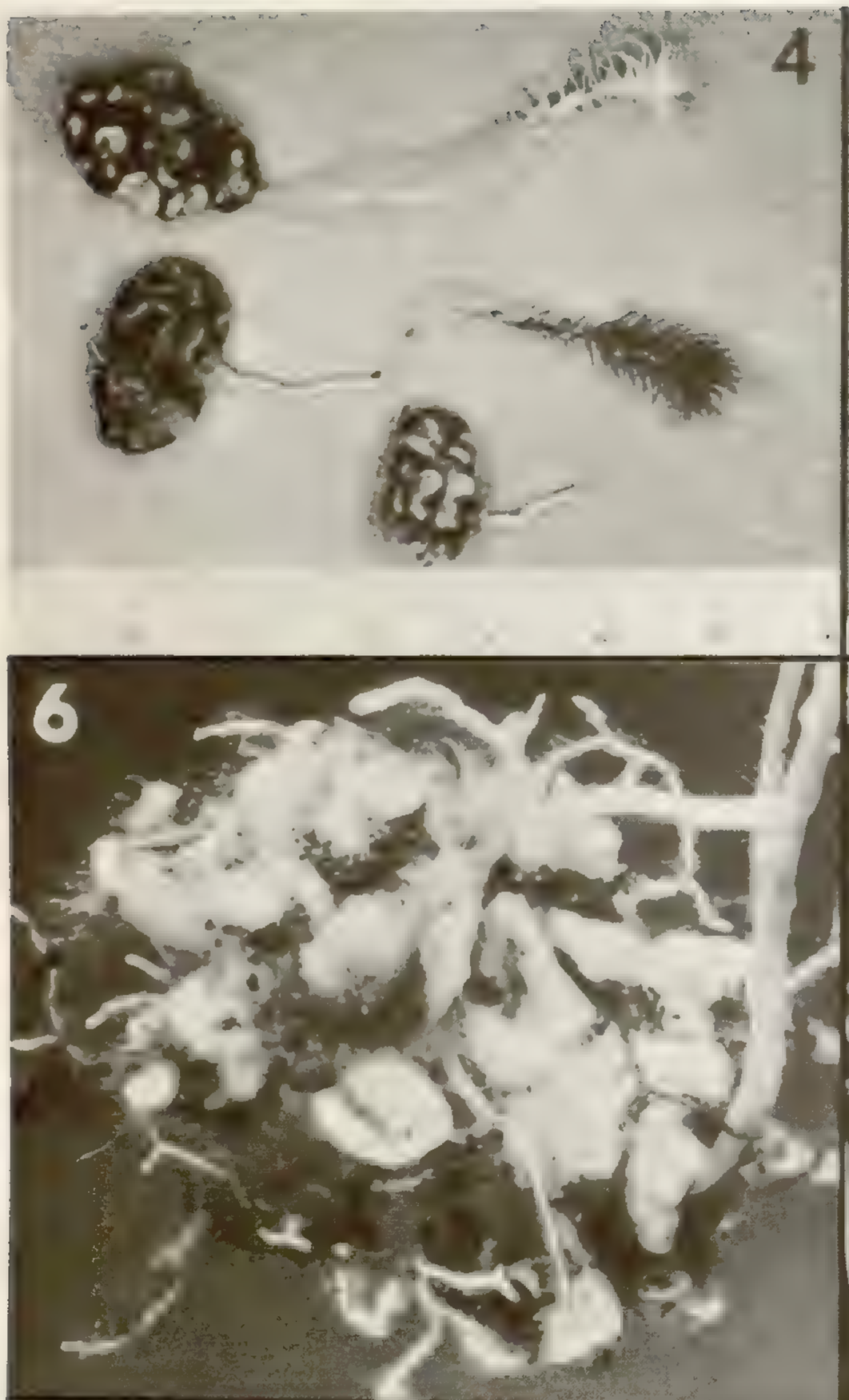
The subterranean gametophytes of other species that have been reported for North America are as follows: *L. annotinum* (Spessard, 1917), *L. clavatum* (Degener, 1924; Gauthier & Dumais, 1938; Spessard, 1917; Stokey & Starr, 1924), *L. complanatum* (Degener, 1924; Eames, 1942; Spessard, 1917; Stokey & Starr, 1924), *L. dendroideum* (Ames, 1926; Degener, 1924; Spessard, 1917, 1922), *L. lucidulum* (Eames, 1942; Spessard, 1917, 1922), and *L. obscurum* (Eames, 1942; Dore, 1945; Gauthier & Dumais, 1938; Stokey & Starr, 1924).

TABLE 1. NUMBER OF *LYCOPODIUM* GAMETOPHYTES AND ATTACHED SPOROPHYTES AT THE JACK PINE PLANTATION SITE.

Species	*Total Number of Gametophytes*	*No. of Attached Sporophytes*		
		0	*1*	*>1*
L. annotinum	1	—	1	—
L. clavatum	70	19	26	25
L. digitatum	136	18	117	1
L. obscurum/dendroideum	144	13	82	49
L. lucidulum	125	39	80	6
Totals:	476	89	306	81

The habitat of the gametophyte we studied is a shrubby JackPine (*Pinus banksiana*) plantation in Mecosta County, Michigan. The plantation was approximately 30 years old in 1977 as determined by tree corings. The trees are spaced 3–4 m apart in rows 4–5 m apart. Occasional irregular spacing apparently is due to the early death of some trees. Black Cherry (*Prunus serotina*) trees, the only other tree associate in the study area (*Fig. 1*), occur in some of the larger spaces. These trees may have persisted since before the pines were planted. The flora is depauperate in understory species. The shrubby species include scattered *Rubus idaeus* and *Comptonia peregrina*. The herbaceous understory consists of *Pteridium aquilinum*, *Carex pensylvanica*, *Rumex acetosella*, *Hieracium* sp., *Monarda fistulosa*, and *Verbascum thapsus*. Associated bryophytes are *Polytrichum juniperinum*, *Brachythecium curtum*, *Pleurozium schreberi*, *Dicranum polysetum*, *D. scoparium*, and *Rhynchostegium serrulatum*. The gametophytes were associated mainly with the more open areas, and particularly with the Black Cherry trees.

The uneven forest floor consists of small knolls and depressions having a difference in elevation of approximately 15–20 cm. The gametophytes generally were associated with the small depressions and the slopes leading into them. In general, the substrate is needle and leaf duff covering a humic layer 1–2 cm thick, which in turn overlies the sandy soil with some humic materials mixed in (*Fig. 3*). The soils in this habitat have been classified as Coloma sands, a transitional soil between the true podsol soils in the northern part of the state and the gray-brown podsolic soils farther south (Wildermuth & Fonder, 1931). The pH of this soil is 5.0.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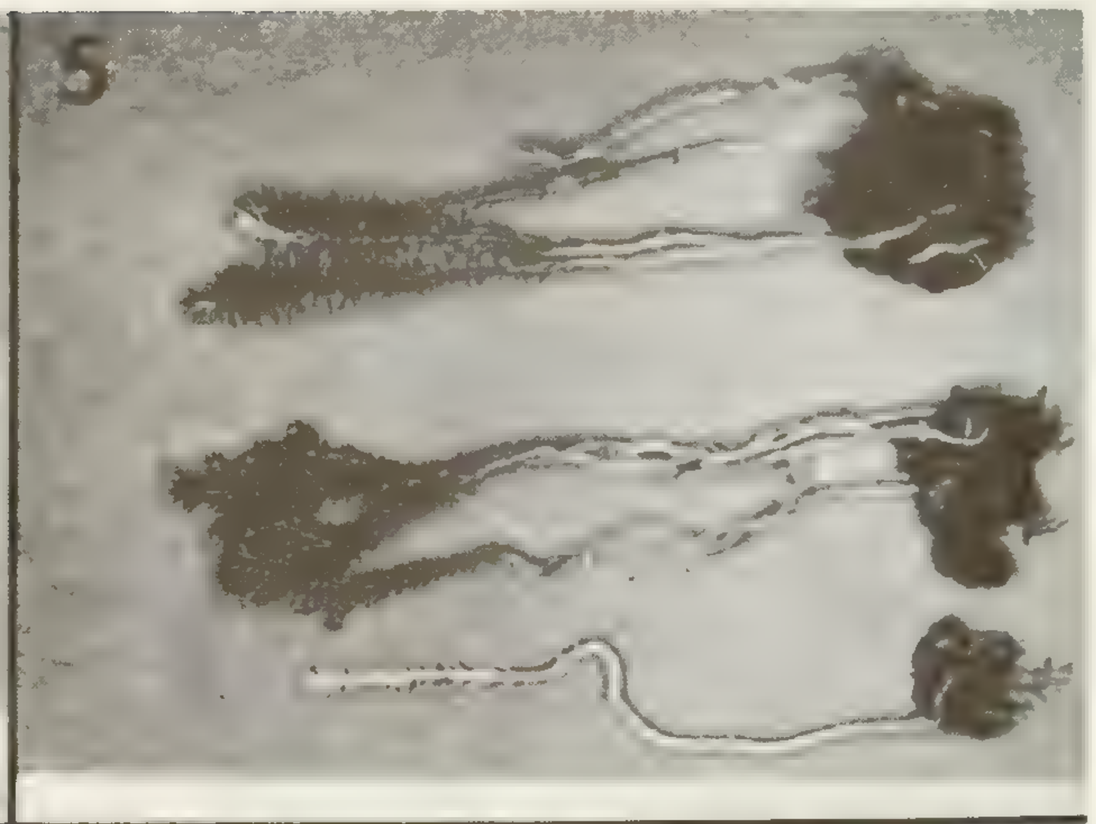
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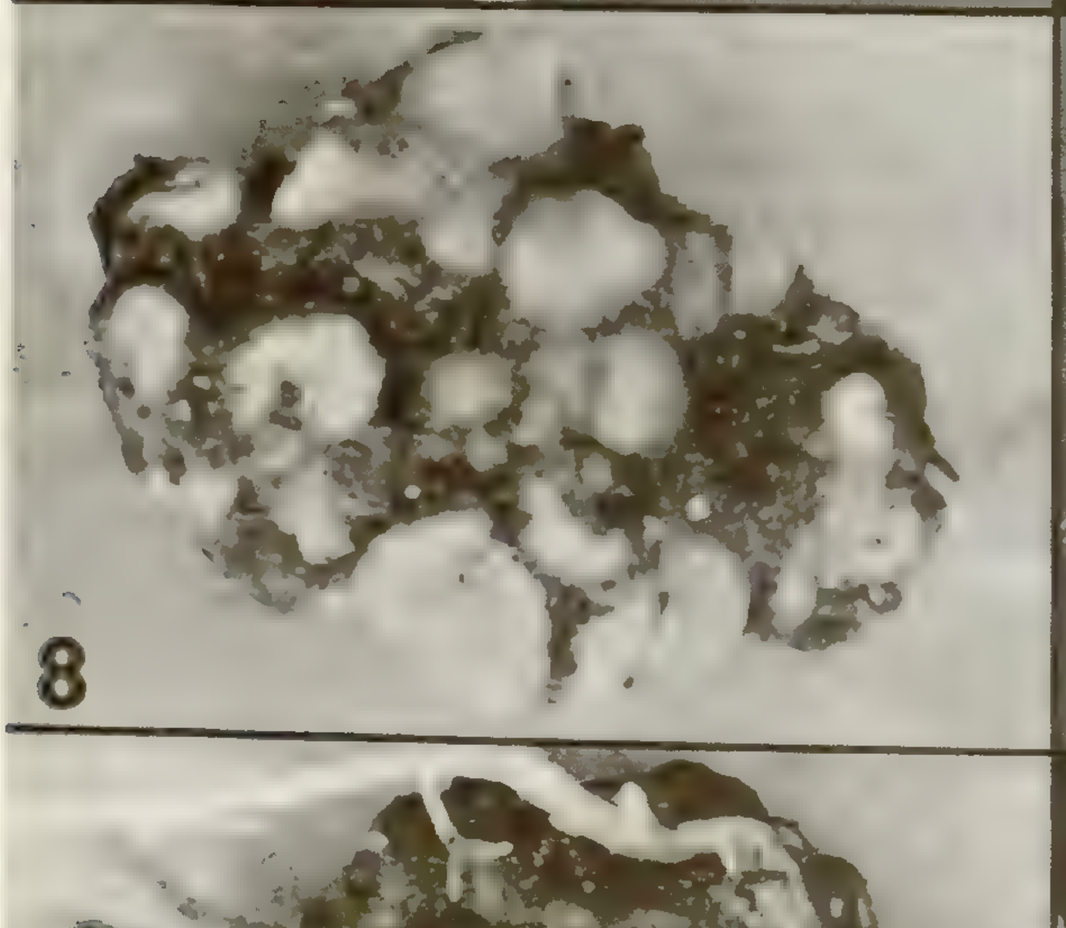
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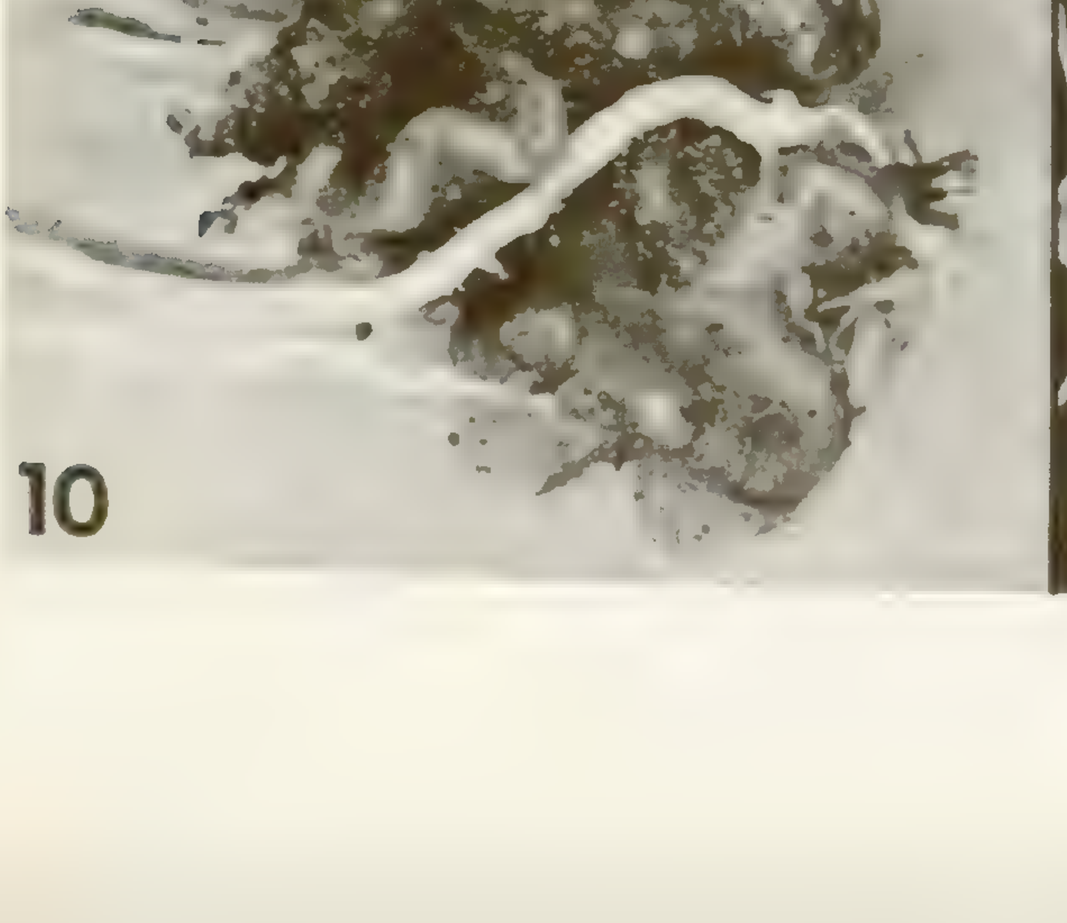
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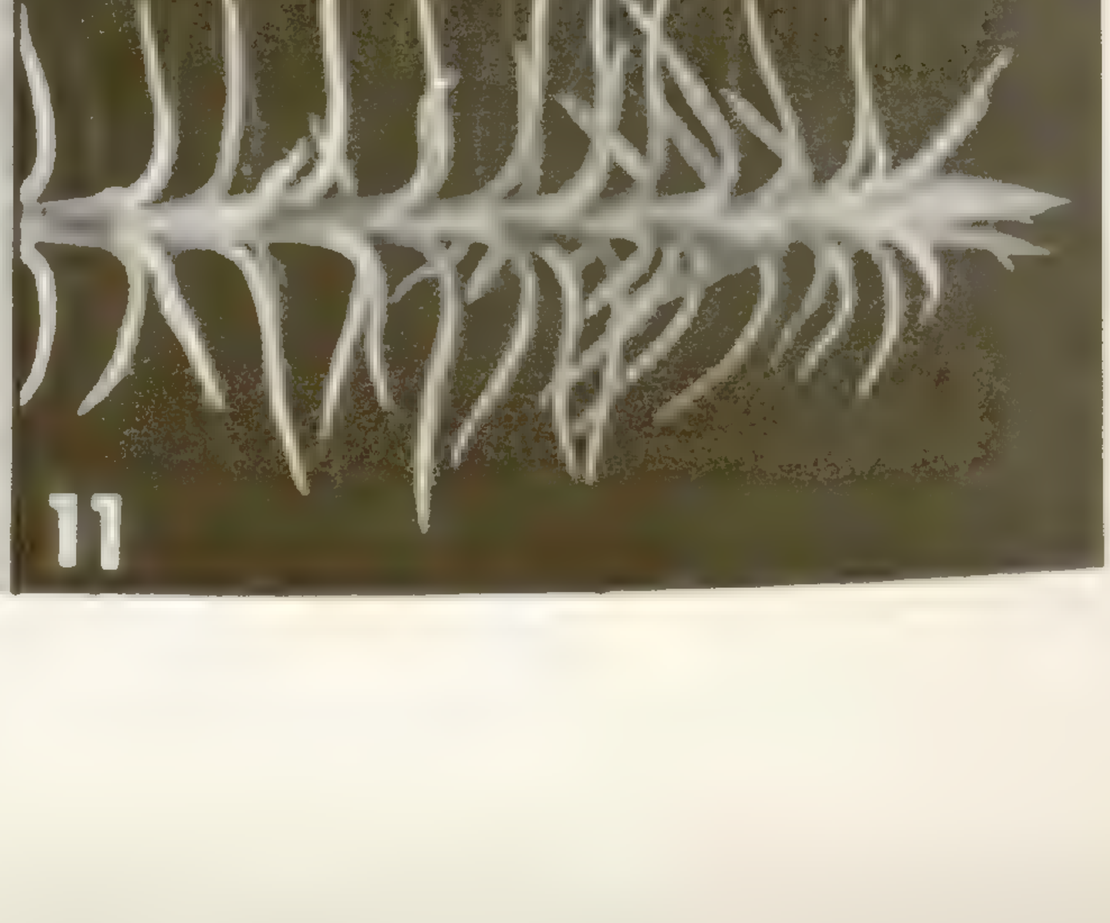
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The number of gametophytes found in each species is listed in *Table 1*. All of the gametophytes appeared to be quite old. Frequently they showed evidence of earlier sporophyte production. In addition, all that we found were relatively large (*Figs. 4–6, 8, 10, 12, 14; Table 2*); and, as shown by Bruchmann (1910), *Lycopodium* gametophytes are believed to grow slowly. Gametophytes and juvenile sporophytes of each species are briefly described below.

Lycopodium annotinum.—Only one gametophyte of *L. annotinum* was found. It was large (*Fig. 6*), highly convoluted, and relatively fragile. Gametophytes of what Bruchmann (1898) called Type I, including in this paper *L. annotinum*, *L. clavatum*, *L. dendroideum*, and *L. obscurum*, all assume a disc shape relatively soon after germination. Then, due to a poorly understood growth mechanism, the edge of the disc convolutes and the gametophyte finally resembles a flat walnut meat. Continuation of this convoluted growth yields the essentially spherical or ovoid masses seen in *Figs. 4–6, 8,* and *10*. The juvenile sporophytes of *L. annotinum* are characterized by fairly elongate leaves (*Fig. 7*) and, in those older than one year, the annular constrictions for which the species is named become readily apparent.

TABLE 2. MAXIMUM DIAMETERS (AND LENGTHS IN *L. FLABELLIFORME*) OF *LYCOPODIUM* GAMETOPHYTES IN mm.

Species	N[1]	$\hat{X}$	*Range*	S.D.
L. annotinum	1	19	19	—
L. clavatum	48	11.2	6–22	3.6
L. dendroideum/obscurum	90	14.2	7–26	4.2
L. digitatum	117	5.5	2.5–13	1.8
		13.8[2]	8–25[2]	3.9[2]

[1] Apparent discrepancies between the number of gametophytes analyzed in this Table and those reported in Table 1 result from omissions in the analysis of injured or broken gametophytes.
[2] Values for gametophyte length.

Lycopodium clavatum.—Numerous gametophytes and young sporophytes of *L. clavatum* were found (*Table 1*). The gametophytes were similar to those of *L. annotinum* in being highly convoluted and relatively fragile (*Fig. 8*). Many gametophytes had multiple sporophytes; indeed, one had 13 attached sporophytes! One albino sporophyte ca. 4 cm long, emergent, and totally devoid of chlorophyll was found (*Fig. 4*). The juvenile sporophytes of *L. clavatum* are easily recognized by the characteristic long hair-tip on their leaves, a feature also found in the adult sporophytes (*Fig. 9*).

FIGS. 4–11. Gametophytes and young sporophytes of *Lycopodium*. FIG. 4. Gametophytes and attached sporophytes of *L. clavatum*. Upper sporophyte albino. Scale in cm. FIG. 5. Gametophytes and attached sporophytes of *L. obscurum/dendroideum*. × 0.5. Lower sporophyte albino. FIG. 6. Gametophyte of *L. annotinum*, ×3. FIG. 7. Young sporophyte of *L. annotinum*. × 3.5. FIG. 8. Gametophyte of *L. clavatum*, ×3. FIG. 9. Young sporophyte of *L. clavatum*. ×3. Note bristle tips on leaves. FIG. 10. Gametophyte of *L. obscurum/dendroideum* with four attached sporophytes. × 2. FIG. 11. Young sporophyte of *L. obscurum/dendroideum*, ×4.5.

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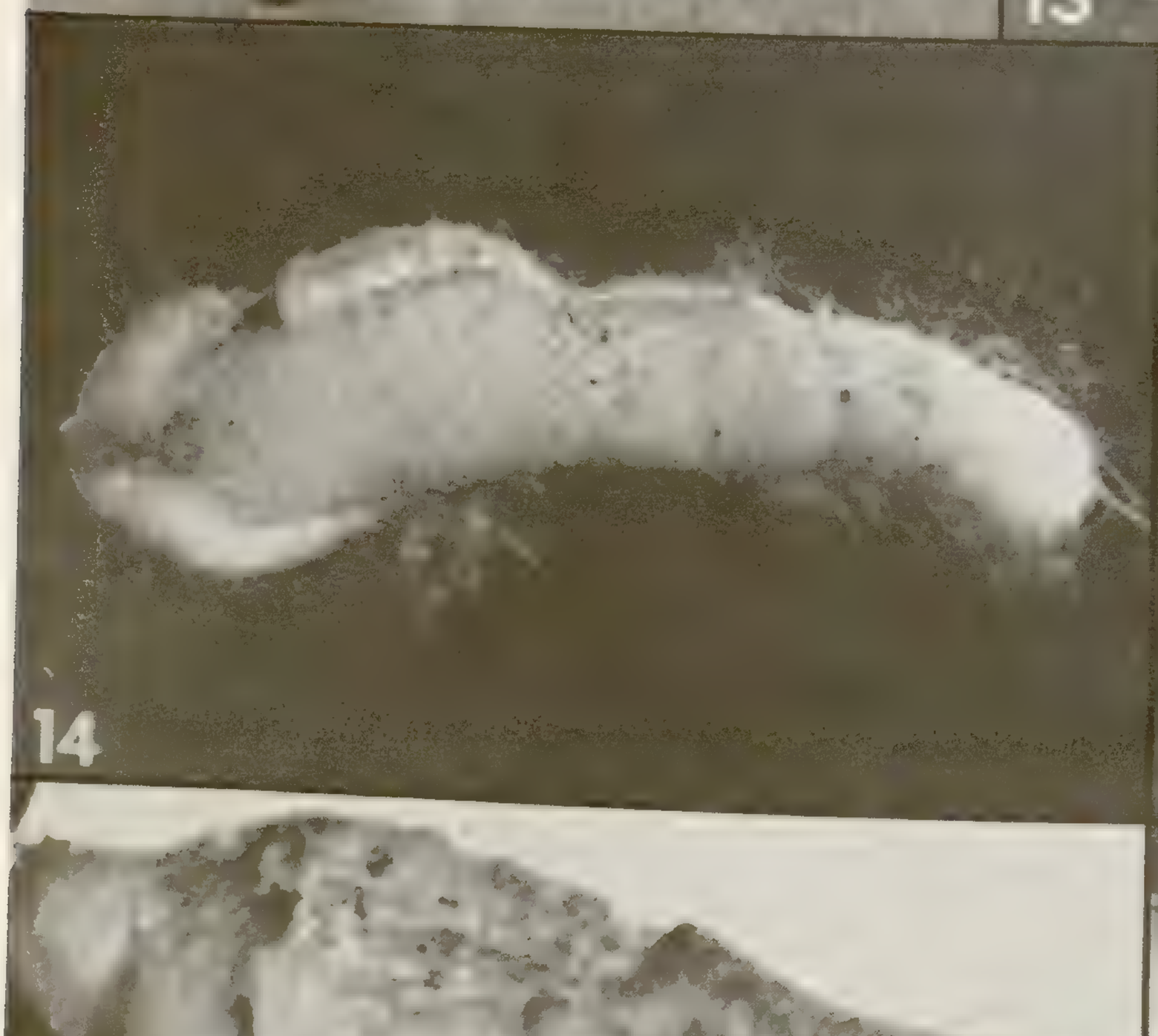
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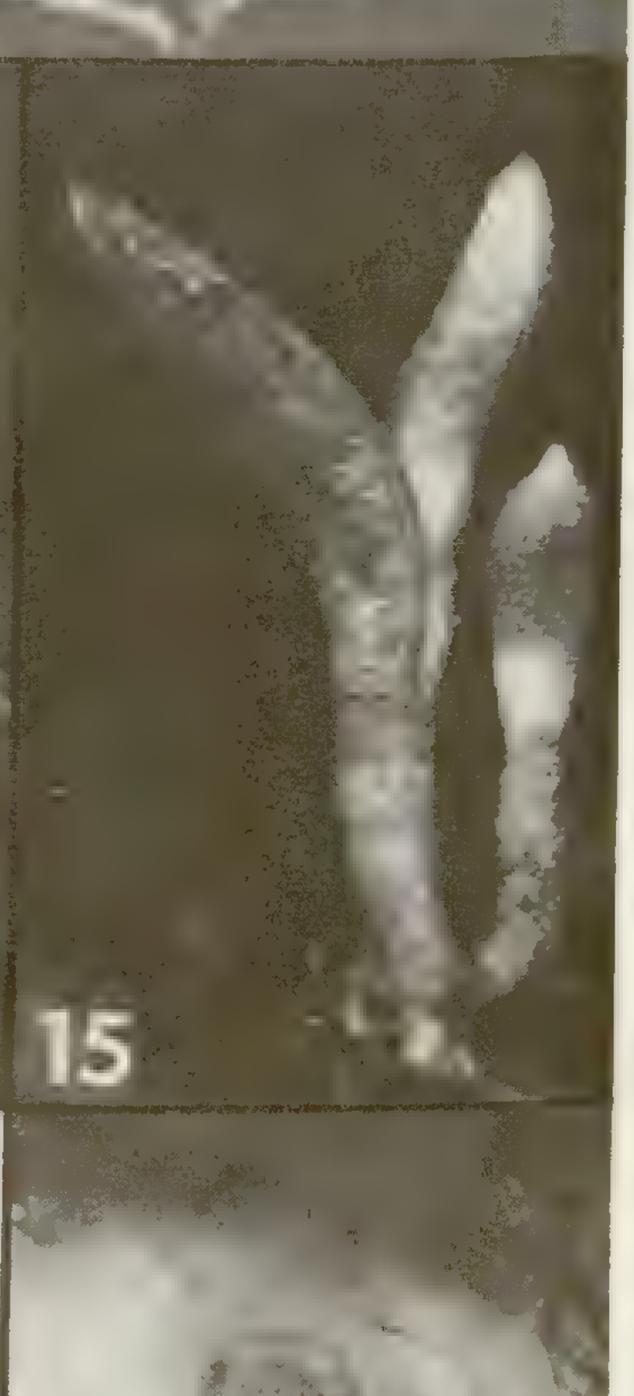
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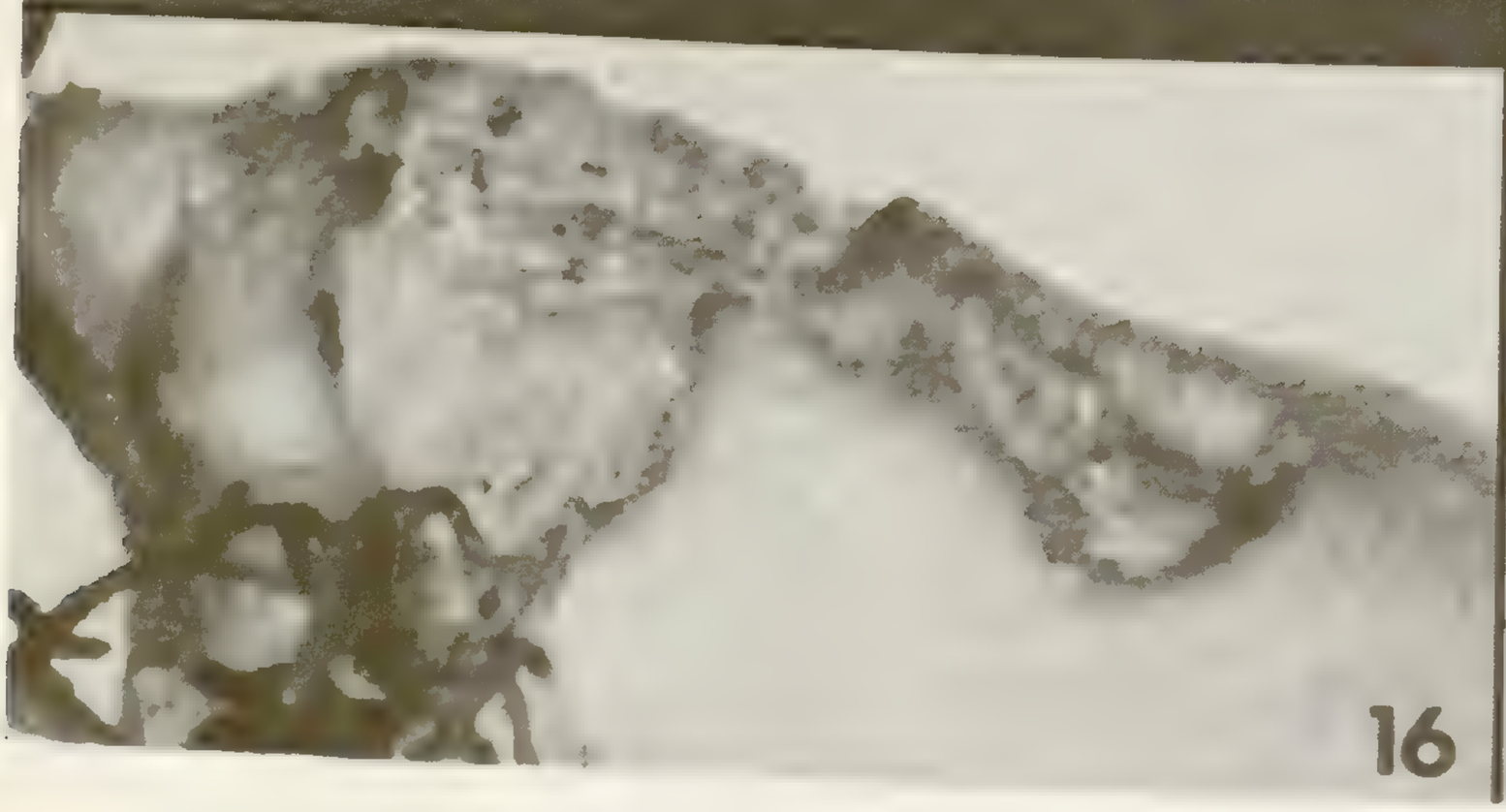
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Lycopodium obscurum and L. dendroideum.—The gametophytes of *L. dendroideum* and *L. obscurum* are here treated together. Although the adult sporophytes of these species are readily distinguishable (Hickey, 1977), we could not distinguish their gametophytes or juvenile sporophytes. Adult sporophytes of both species occurred within the locality, but *L. obscurum* was by far the more common. The gametophytes were similar to those of the two preceding species in that they were convoluted (*Fig. 10*), but the convolutions were very coarse and the gametophytes, in contrast to those of *L. annotinum* and *L. clavatum*, were firm and sturdy.

The young sporophytes' leaves lacked the bristle tip of those of *L. clavatum* and generally were shorter than those of *L. annotinum*. However, the young sporophytes were surprisingly similar to those of *L. digitatum* (cf. *Figs. 11* and *13*).

Lycopodium obscurum/dendroideum yielded the most abundant gametophytes and young sporophytes (*Table 1*). Multiple sporophytes were common, as in *L. clavatum*, and in one case ten sporophytes were attached to a single gametophyte. Also as in *L. clavatum*, one albino sporophyte was found (*Fig. 5*). It was emergent, ca. 6.5 cm long, and totally devoid of chlorophyll.

Lycopodium digitatum.—Numerous specimens of *L. digitatum*[1] gametophytes and young sporophytes were found (*Table 1*). The distinctive carrot shape of the gametophytes (*Fig. 12*) makes them readily identifiable. All intermediate stages in the development of sporophytes from very young with little or no chlorophyllous tissue to those exhibiting the characters of the adult flat-branched sporophytes were present. Although these plants could have been the similar *L. complanatum*, no sporophytes of that species were seen at the locality, and the nearest known locality is well over 100 miles north of the site. We cannot rule out the possibility that some of the carrot-shaped gametophytes without attached sporophytes might have been *L. tristachyum*, but we consider this to be unlikely. Only one unattached, possibly three- or four-year old sporophyte plant of the closely related *L. tristachyum* was seen. Its distinctive, bluish-green color was in conspicuous contrast to the darker green of *L. digitatum*.

Some *L. digitatum* gametophytes appeared to have been partly eaten (*Fig. 16*). Most gametophytes had only a solitary attached sporophyte, although one specimen had five. Orientation of the gametophyte was apparently random and seemingly did not affect sporophyte production.

---

[1] Hickey and Beitel (1979) recently determined that *L. digitatum* A. Braun is the correct name for the species formerly called *L. flabelliforme* (Fern.) Blanch. or *L. complanatum* var. *flabelliforme* Fern.

FIGS. 12–17. Gametophytes and young sporophytes of *Lycopodium*. FIG. 12. Gametophytes of *L. digitatum*, ×4. FIG. 13. Young sporophyte of *L. digitatum*, ×5. FIG. 14. Gametophyte of *L. lucidulum*, dorsal surface, ×5. FIG. 15. Young sporophyte of *L. lucidulum*, ×10. FIG. 16. Gametophyte of *L. digitatum* damaged by predator. Axis of gametophyte oriented horizontally, damage on flank below meristem which is at left, ×16.5. FIG. 17. Gametophyte of *L. digitatum* with circular scar showing old connection of foot to main axis of sporophyte, ×25.

Young sporophytes were essentially indistinguishable from those of *L. obscurum/dendroideum* (cf. *Figs. 11* and *13*). However, as soon as the young sporophytes began to branch, phyllotactic changes took place that culminated in plants with essentially adult foliage, going from spiral to falsely opposite.

Lycopodium lucidulum.—The gametophytes of *L. lucidulum*, although generally axially elongated, had definite upper and lower surfaces (*Fig. 14*). A peculiar feature of these gametophytes was that all 125 of them came from a small square of ground roughly 45 cm on a side. Furthermore, these gametophytes occurred in an upland, well drained site, whereas the nearest adult sporophytes were in a white cedar bog approximately one half mile away. The gametophytes were particularly distinctive at the microscopic level because of the presence of multicellular, uniseriate paraphyses associated with the gametangia. The young sporophytes had rather boat shaped leaves with minutely toothed margins (*Fig. 15*).

GAMETOPHYTE SIZE AND LONGEVITY

One striking characteristic of the gametophyte community in the JackPine woods was the total absence of reproductively mature sporophytes. The habitat is several acres in size and is bordered by areas which do possess mature sporophytes.

Coincident with the lack of mature sporophytes was the apparent old age of the gametophytes. This observation is inductive and is based on the large size of the gametophytes, their presumed slow rate of growth, and the evidence of previous sporophyte production (*Fig. 17*). The assessment of old age is bolstered by Bruchmann's observations (1910) on European species with subterranean gametophytes in which he was able to ascertain ages of 3–8 years preceding reproductive maturity. Our observations over a four year period show that the gametophytes produce numerous sporophytes. These results suggest premature death of the young sporophytes, more of which are produced each year. Based on long observations, Eames (1942) allowed ten years for gametophyte production in the habitats he studied. Yet, the presumed old age of the gametophytes suggests that our site could have been favorable for growth of these gametophytes since the pine plantation was founded some 30 years preceding this report.

One further observation of relevance here is the fact that no small gametophytes were found (*Table 2*). In other sites that we have investigated, numerous gametophytes have been recovered that were not only producing young sporophytes, but were all smaller than any of the gametophytes at the present site.

These observations suggest that current conditions are not favorable for spore arrival and/or germination, nor apparently have they been for some time. Nevertheless, the present conditions are ideal for continued gametophyte growth and maintenance. The present conditions are also apparently ideal for sporophyte production, but are very poor for continued sporophyte growth and maintenance.

The habitat is successional in nature, although it is an artificial plantation. Both Spessard (1917) and Eames (1942) noted that successional habitats are the most frequent kind of site in which *Lycopodium* gametophytes grow.

Gametophyte clustering was seen for all species studied here, with the exception of *L. annotinum*, which was found in numbers too small to be relevant. The most spectacular case was *L. lucidulum*, with all 125 gametophytes from a square 45 cm on a side. Spessard (1922) noted similar occurrences of *L. lucidulum*, as well as less spectacular finds of other species. The clustering of gametophytes has also been noted in *Botrychium* (W. H. Wagner, U. of Michigan, pers. comm.). While this is regarded as a feature of special note, it should be remembered that pteridophytes with surficial gametophytes also illustrate striking clustering. However, in the case of the surficial gametophytes, the microenvironmental features controlling population size and distribution, such as moisture, protection, and shading, frequently are more obvious. It seems reasonable that microenvironmental features might also control population distribution in subterranean gametophytes as well. However, in the latter case, the environmental features are much less obvious, such as distribution of mycorrhizal fungi.

We wish to express our appreciation to W. H. Wagner, Jr., for help and support during portions of this study, to William R. Buck for verifying the identifications of the Bryophytes, to Randy O. Wayne for numerical analysis of the gametophytes of *L. digitatum*, and to Ellen and Lee Weatherbee without whom we would never have made this discovery.

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Acrostichum in Florida

DAVID C. ADAMS* and P. B. TOMLINSON**

This article is the result of field study of several *Acrostichum aureum* L. and *A. danaeifolium* Langsd. & Fisch. populations in the swamps of South Florida. It was made with the object of establishing consistently applicable diagnostic differences between these oftimes confused species. Our observations will facilitate field identification, and we also have found some pertinent ecological differences between the two species.

No attempt has been made to resolve the possibly more complex problem of *Acrostichum* in the Asian tropics, where in addition to two distinct and widely distributed species (Troll, 1933), there may be locally differentiated forms which have remained insufficiently examined, as in New Caledonia.

The differential characteristics which our study has elucidated are summarized in the following key:

Axis usually creeping, relatively frequently branched. Fertile fronds with only the upper pinnae (up to 5 pairs and the terminal pinna) fertile (*Fig. 1A*). Pinnae few, usually not more than 30, rather distant and often irregularly distributed, usually not overlapping, the lowest pinnae always distant, long-stalked (up to 3 cm) (*Fig. 1C*). Areoles next to the midrib narrow, always 3 times longer than wide. Rachis rounded below, decidedly grooved above with the margin of the groove acute, and with short spines (the midribs of aborted pinnae) frequent on the lower part of the rachis (*Figs. 1B, D*). Basal scales not leaving prominent scars (*Fig. 1E*). Paraphyses with a slender stalk, ending in a single, ± isodiametric, irregularly much-lobed cell (*Fig. 1F*). ..... *A. aureum*

Axis usually erect, relatively infrequently branched. Fertile fronds with all or most of the pinnae fertile, rarely only a few upper ones fertile (*Figs. 2G, H*). Pinnae many, usually 40–60, closely set, overlapping and regularly arranged (*Fig. 2A*), often subopposite, the lowest pinnae relatively short-stalked (less than 2 cm) (*Fig. 2E*). Areoles next to the midrib broad, never more than 3 times longer than wide (*Fig. 2D*). Rachis with several shallow grooves below, flat or scarcely grooved above, with the margins of the groove blunt (*Fig. 2E*), and with basal spines or aborted pinnae absent (*Figs. 2B, H*). Basal scales leaving prominent scars (*Fig. 2F*). Paraphyses with the stalk ending in a horizontally extended, smooth or little-lobed cell (*Fig. 2I*) ..... *A. danaeifolium*

The best characters for distinguishing the species are found in features of the whole frond and in the difference in distribution of fertile pinnae. These differences and general features of ecology were well appreciated by Small (1931). Jenman (1909) also gave a good account of the two species, and many contrasting features are clearly recognized by García de López (1978).

The marginal spines of *A. aureum* are very distinctive when present. Paraphyses provide an excellent diagnostic feature for fragmentary fertile herbarium specimens. Neither areole size and overall orientation nor leaflet shape seem consistently useful, although these characters were emphasized both by Small (1931, p. 237) and by Wherry (1964), except for the difference in length of areoles

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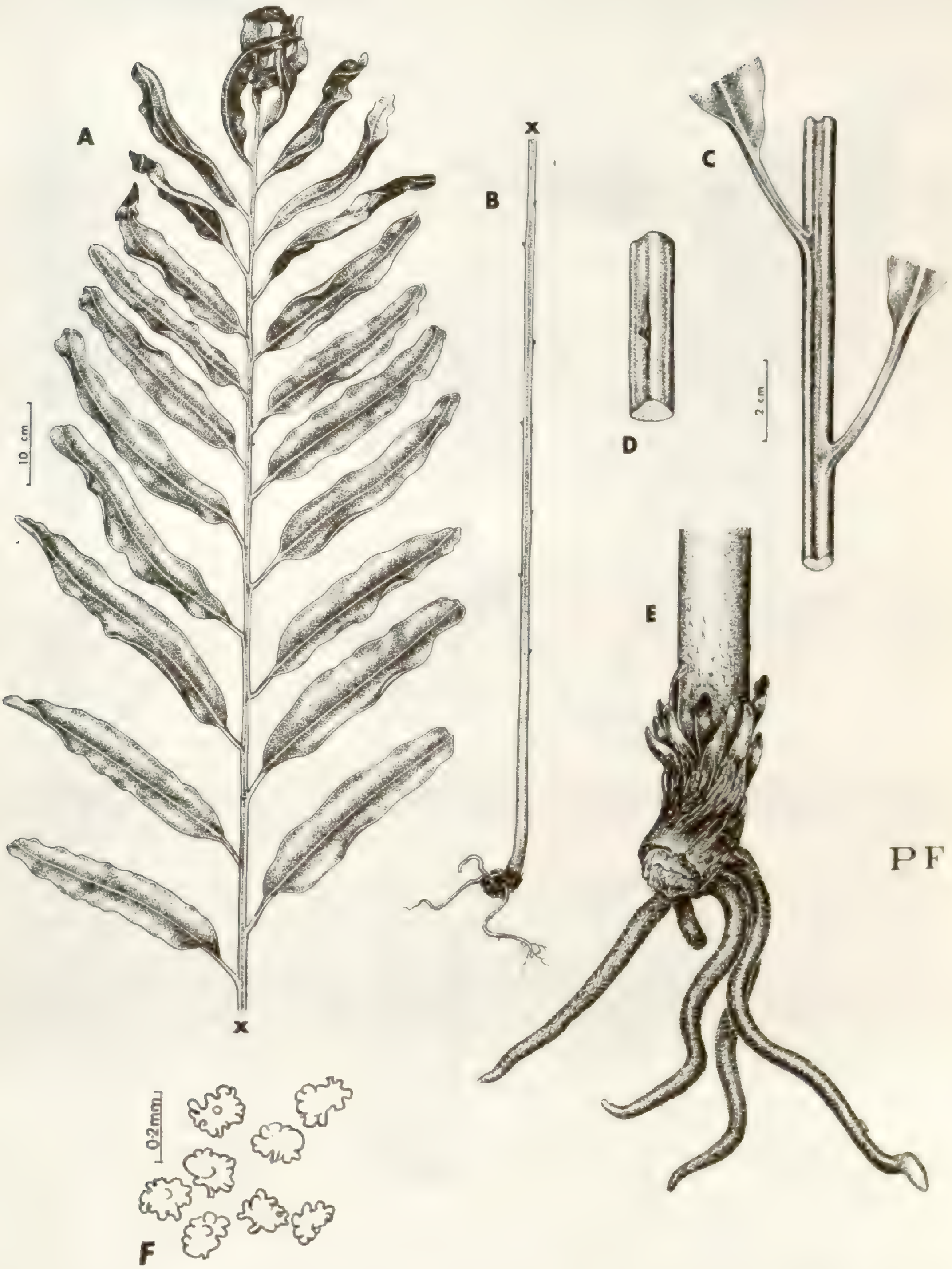

FIG. 1. *Acrostichum aureum*. FIG. 1A. Upper part of frond. FIG. 1B. Lower part of frond. FIG. 1C. Middle of frond showing pinnule attachment. FIG. 1D. Part of leaf axis with a marginal spine. FIG. 1E. Leaf base with adventitious roots and scales. FIG. 1F. Paraphyses.

FIG. 2. *Acrostichum danaeifolium*. FIG. 2A. Upper part of sterile frond. FIG. 2B. Unarmed axis of sterile frond. FIG. 2C. Single pinna. FIG. 2D. Areoles in midrib region. FIG. 2E. Middle of frond showing pinnule attachment. FIG. 2F. Base of leaf axis with persistent scale scars. FIG. 2G. Upper part of fertile frond. FIG. 2H. Lower part of fertile frond. FIG. 2I. Paraphyses.

next to the midrib. The leaflets in *A. aureum* seem somewhat more thickly coriaceous than in *A. danaeifolium*, but textural differences are difficult to assess in herbarium specimens. There are no immediately obvious differences in sporangium size or spore diameter. The SEM photographs of García de López (1978) indicate that the wall sculpturing of the spores also is identical.

Leaf dimensions are variable, but *A. aureum* seems to be the smaller species. In the populations examined, the more erect axis of *A. danaeifolium* leads to a closer aggregation of leaves, which seems consistent but requires verification in other parts of the species' range. In this respect, *A. aureum* seems better adapted to vegetative persistence because of its more frequent branching.

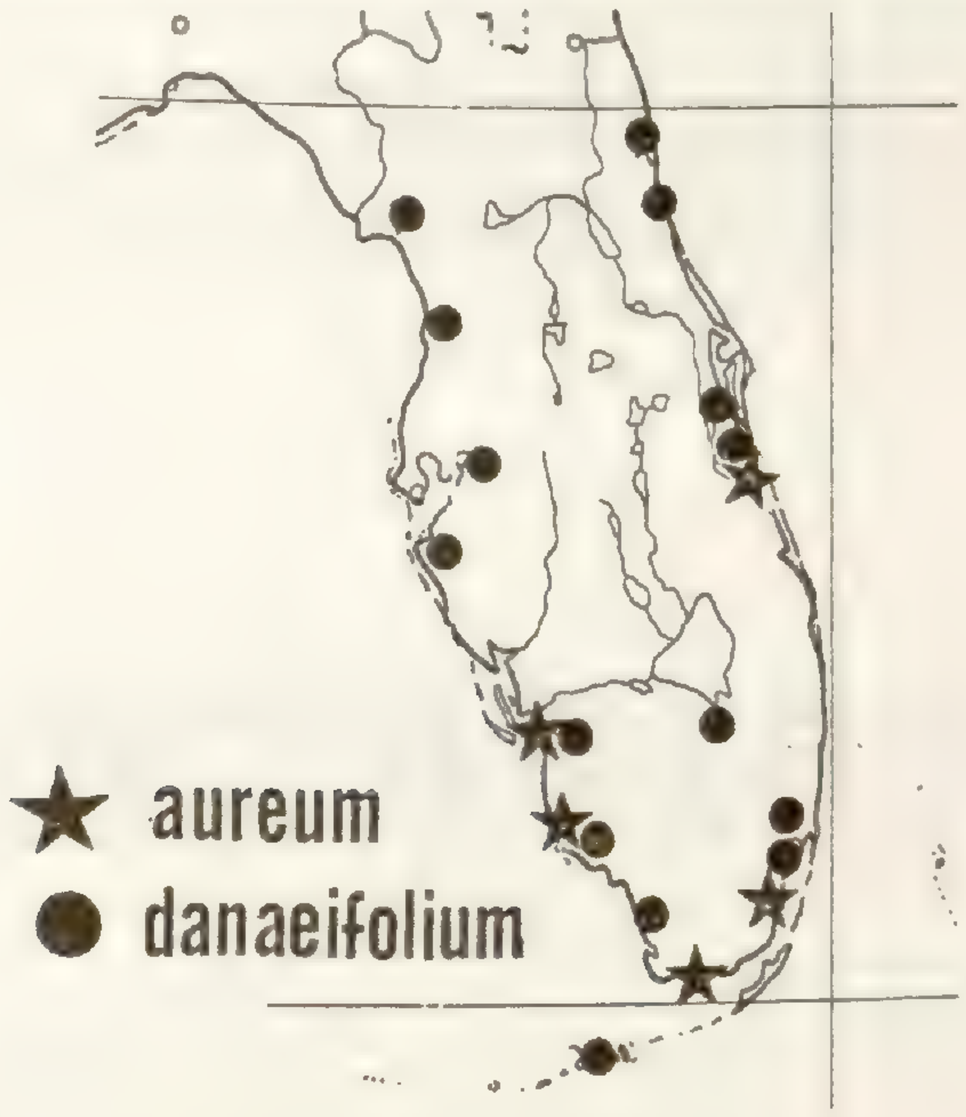

FIG. 3. Distribution of *Acrostichum* in South Florida based on specimens in the Harvard University Herbaria and field observations.

In South Florida, *A. aureum* is the less common species and is seemingly restricted to the saline muck of back-mangrove communities, as suggested by its coastal distribution (*Fig. 3*). *Acrostichum danaeifolium* is the more common species and occurs both in saline substrates of back-mangroves and also extends inland to fresh-water swamps, commonly in sink-holes in hammocks. It also is a plant of disturbed marl sites and has weedy tendencies. The greater range (*Fig. 3*) and wider edaphic tolerance of this species may be due in part to its greater resistance, which in turn may be related to its more condensed crown of leaves.

In our experience, both species, but especially *A. danaeifolium*, have a wide tolerance for light conditions but seem most vigorous in full sun. They can occur together at the same site, but in our experience show no evidence of hybridization. However, García de López (1978) mentions intermediate forms which she considers to be hybrids in the Dominican Republic. Sown spores of both species germinate readily and produce sporelings without manipulation. Since the reproductive parts are large and easily studied microscopically, *Acrostichum* would make an excellent subject for studies of the fern life cycle.

This study was initiated as a class project in the "Plants of the Tropics" biology class taught at Fairchild Tropical Garden in 1976, with support from the Atkins Garden Fund of Harvard University. We are indebted to Don Evans, George Avery, and Rolla Tryon for comments and field assistance and to the Director, Gray Herbarium of Harvard University, for access to the collections.

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Phyllitis scolopendrium Newly Discovered in Alabama

JOHN W. SHORT*

Long known as one of the rarest ferns in North America, the American Hart's-tongue, *Phyllitis scolopendrium* var. *americanum* Fern., has been reported from New Brunswick, Ontario, New York, Michigan, and Tennessee (Wherry, 1961). It has been reported from two localities in Tennessee (Shaver, 1954). The first plants were found at a cave mouth in Roan County in 1849, but they had disappeared by 1900. The second site, discovered in 1878 a few miles north of Bridgeport, Alabama, in a lime sink in Marion County, Tennessee, contained plants which are surviving but are underdeveloped. The Hart's-tongue has not been found elsewhere in the southeastern United States until now.

In early October 1978, E. Batchelder, a co-worker of the author and an avid spelunker, told of a caving expedition to Jackson County, Alabama, the previous weekend. While entering a cave through a deep sink, he saw an unusual-looking fern and photographed it. Two weeks later the photograph had been developed, and the fern proved to be *P. scolopendrium*.

The site was visited on October 21 by a group consisting of the author, Mr. Batchelder, C. Batchelder, J. Shearon, M. Shearon, and D. Gazaway. The sink is about a mile from the village of Paint Rock on the western flank of Nat Mountain at about 1200 feet elevation. The sink is about 40 feet deep and its walls are vertical or overhanging, except for a narrow cleft through which passes a path so steep that a rope is necessary to enter the sink. There are also two cave mouths at the bottom.

A small but thriving colony of *P. scolopendrium* was found at the bottom of this sink. Twenty plants were observed on this and subsequent visits. During a second visit on November 24, it was found that one of the plants had been destroyed by some person who apparently had slid off the main path to one of the caves and slid down the steep slope where the ferns were growing. *Athyrium pycnocarpon*, *Asplenium rhizophyllum*, and *Cystopteris tennesseensis* were also found in this sink.

Eight of the Hart's-tongue plants were mature adults, including a few which were quite robust. The rest were juveniles of various apparent ages. The ferns were growing on rocks or in soft, black soil. One adult was on a ledge a few feet above the sink bottom. The *Phyllitis* plants were photographed and a number of leaves were collected as vouchers (*Short 1187*). These specimens are being distributed to various herbaria, including AUA, MICH, TENN, UNA, US, and VDB.

On the slopes of the mountain and in a nearby sink were found a number of other fern species, including *Adiantum pedatum*, *Asplenium platyneuron*, *A. resiliens*, *Pellaea atropurpurea*, *Polypodium polypodioides*, *Polystichum acrostichoides*, and *Woodsia obtusa*.

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Nat Mountain is about 40 miles southwest of the Marion County, Tennessee, locality in a large area of rugged terrain formed by stream dissection of the Cumberland Plateau. The mountains, actually mesas, rise to elevations of 1600–1700 feet, about 1000 feet above the surrounding flat-bottomed valleys. The slopes are limestone with thin sandstone caps. This heavily forested, largely inaccessible area comprising the section of Alabama east of Huntsville and north of the Tennessee River has been little explored by botanists, even though some nearby areas have received considerable attention. It would seem that *P. scolopendrium* may be present at other suitable locations in this area. Indeed, E. T. Varnedoe, another experienced spelunker, saw Mr. Batchelder's photograph and was of the opinion that she had seen the fern in several such places in Jackson and Madison Counties.

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REVIEW

"SYNAPTOSPORY: A HYPOTHESIS," by K. U. Kramer, Gard. Bull. 30:79–83. 1977.—It has been known for a long time that certain pteridophytes shed their spores in small groups or in tetrads and that others disperse whole sporangia, some with the spores already germinating inside. Not much thought has been given to the biological or evolutionary importance of this phenomenon, which Kramer has termed synaptospory.

Kramer suggests that the function of sculptured perispores is to increase the chance of synaptospory. This makes it likely that gametophytes will grow close together and that inter-gametophytic selfing will occur. Such cross-fertilization tends to maintain genetic diversity and to reduce the expression of recessive deleterious genes.

Synaptospory tends to be found in terrestrial ferns, which are long-lived and grow mostly in extensive, stable habitats. Dispersal of such species at a distance is of relatively little consequence to their evolutionary success because of their stable habitats.

Epiphytic ferns, on the other hand, commonly lack a visible perispore and do not exhibit synaptospory. (The perispore of these ferns is not really lacking, but rather is tightly adherent to the exine, as demonstrated by electron microscopy.) The habitat of epiphytic ferns is minute, short-lived, and unstable. Epiphytic ferns tend to occupy their immediate habitat by means of creeping rhizomes. But their need over the long term is to spread to similar but non-adjacent habitats, and single-spore dispersal accomplishes this better than synaptospory.—*D. B. L.*

Studies in Lycopodiaceae, II. The Branching Patterns and Infrageneric Groups of Lycopodium sensu lato

B. ØLLGAARD*

Several contributions of *Lycopodium* taxonomy on the infrageneric level have been made recently (Wilce, 1965, 1972; Chu, 1974; Ollgaard, 1975; Bruce, 1976a, b, c). Earlier literature on the classification of this group was summarized by Wilce (1965) and Bruce (1976b) and need not be repeated here. The present study includes new observations on branching patterns and attempts to correlate these with infrageneric classifications of *Lycopodium*, about which there has been some disagreement. Only Troll (1937, pp. 465–482) has dealt with the subject at some length considering the genus as a whole; other students (Holloway, 1916, 1919; Wilce, 1965; Primack, 1973) have treated smaller groups in greater detail.

MATERIALS

The present study is based on field observations made in various parts of Europe and during two expeditions to Ecuador in 1973 and 1976 (Holm-Nielsen et al., 1975; Øllgaard & Balslev, 1979). In addition, herbarium specimens representing a large number of species, mainly from Ecuador, have been studied from several herbaria (A, B, BM, CAS, DS, E, F, G, GB, GH, K, MSC, NY, OXF, P, S, UC, and US) in preparing a treatment of the Lycopodiaceae for the "Flora of Ecuador." Material from other parts of the world has mainly been studied in the Botanical Museum, Copenhagen (C), the Herbarium Jutlandicum (AAU), and the Museum of Natural History, Stockholm (S). I am indebted to the curators of the institutions mentioned above for permission to study the specimens in their care. Special thanks are due to Dr. D. R. Given, Christchurch, New Zealand, for material of *Lycopodium laterale* R. Br., and to Mr. John Woodhams, Royal Botanic Gardens, Kew, for a specimen of *L. nummularifolium* Blume. I wish to express my gratitude to the Danish Natural Science Research Council for support for my field work in Ecuador in 1976.

In the following text, the infrageneric groups correspond to those of Wilce (1972), unless otherwise stated. For nomenclatural reasons, some of the names used by Wilce have been changed: Subg. *Urostachya* Pritzel is the original spelling, and should be retained, not *Urostachys*.[1] Subgenus *Lycopodiella* (Holub) Øllgaard[2] comprises the species included in subg. *Lepidotis* (Palisot) Baker by Wilce. Since the name *Lepidotis* is a nomen confusum, as stated by Holub (1964), the generic name *Lycopodiella* is here made available at the subgeneric level.

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[1]Herter (Bot. Jahrb. Engler 43, Beibl. 98:5, 29, 30. 1909) illegitimately altered *Lycopodium* subg. *Urostachya* Pritzel. Later he (Beih. Bot. Centralbl. 39(2):249. 1922) effectively made a new genus *Urostachys* Herter, which is correctly spelled with a terminal *-s*.—*Ed.*

[2]*Lycopodium* subg. **Lycopodiella** (Holub) B. Ollgaard, comb. nov. Basionym: *Lycopodiella* Holub, Preslia 36:20, 22. 1964.

BRANCHING PATTERNS IN LYCOPODIUM

The genus *Lycopodium* commonly is used as an illustration of dichotomous branching in vascular plants. Indeed, dichotomy is the basic mode of branching in this genus, although lateral branching is a regular event in at least one species and occurs less regularly in others. Trichotomy, which is similar to dichotomy but results in three branches, occurs more randomly.

Usually the descriptions of the vegetative body of *Lycopodium* apply a number of terms which were originally coined for plants with lateral branching, such as sympodial and monopodial branching, main and lateral branches, or principal and secondary branches. Such terms are in principle inaccurate or incorrect for plants in which minor and major branches must be considered ontogenetically equivalent. However, the establishment of a terminology which is both accurate, correct, and practical is hardly possible in a genus with such diverse and plastic patterns. In this paper, I use the term main to indicate a function of an axis, but avoid the terms principal, secondary, and lateral, except where they are properly applied in cases of true lateral branching.

The variation in Lycopodiaceae branching patterns is mainly due to three variable characters, as enumerated below.

Relative size of branches of dichotomies.—The branches of a dichotomy may have equal or unequal diameters. The terms isotomy and anisotomy for these conditions were introduced by Troll (1937, pp. 468–469). Since equal branch diameter is the sole criterion for isotomy, it follows that isotomous branches may differ in length, function, or both. Correspondingly, anisotomy was defined by Troll as dichotomy leading to unequally thick branches resulting from unequal branch primordia. A precise distinction between anisotomy and isotomy sometimes is difficult, although the smaller branch of an anisotomy usually is recognized by its reduction in both diameter and length.

A general feature of anisotomous species is the formation of one or more main axes functioning as rhizomes or aerial main stems. This is achieved through the regular alternation of major and minor branch primordium positions in successive dichotomies. This is the dichopodial branching of Bock (1962); more commonly it is termed pseudomonopodial branching. Overtopping in the major branch and development of the minor branches into shorter and more or less determinate branches or branchlet systems complete the development.

Orientation of successive branching planes.—Branchings may occur in planes successively perpendicular to one another, in a single plane, or may form other angles in relation to each other. Following Troll (1937, p. 474), the first two conditions are termed cruciate and flabellate, and the third is here termed inclinate. Many species display combinations of these conditions, often in fixed sequences in connection with certain events in their development.

Observations of these characters are made with some difficulty. Herbarium material is often inadequate because of distortion as a result of pressing. Living plants also may be distorted. The so-called erect species usually are erect only when quite young. Later they overturn under the increasing weight of the plant,

the stem base becomes decumbent, and the branch apices turn upwards. In specimens with long, lax, pendant stems, the orientation is affected by contact with adjacent stems. In both cases, precise observation of branch orientation is complicated or impossible, but often it is possible to find short sequences of branches which are characteristic.

Functional differentiation.—The branches of a dichotomy may be completely similar in function, or a branch-pair may differentiate into one vegetative and one fertile branch, into one rhizomatous and one aerial branch, and so on.

SUBGENUS UROSTACHYA

This group contains probably more than 400 mainly tropical, entirely isotomous species. About a third are terrestrial; the others are mostly erect or pendant epiphytes.

It has been argued that the bulbils formed in *L. selago* L., *L. lucidulum* Michx., etc. are examples of extreme anisotomous branching (Bierhorst, 1971, p. 9). But according to other views (reviewed in Cutter, 1966), they are foliar in origin. The capacity to form bulbils may be a character of taxonomic significance in subg. *Urostachya*, but it is not further considered in this study.

In the majority of species, branch length and development is almost identical. This is especially true for a great number of terrestrial species. Many pendant epiphytes vary with respect to branch length and corresponding branching intervals. This probably is an adaptation of individual branches to different light intensities in large plants, which may develop hundreds of branches from a single basal stem. However, the branch diameters are the same in corresponding long and short branch intervals of such individuals.

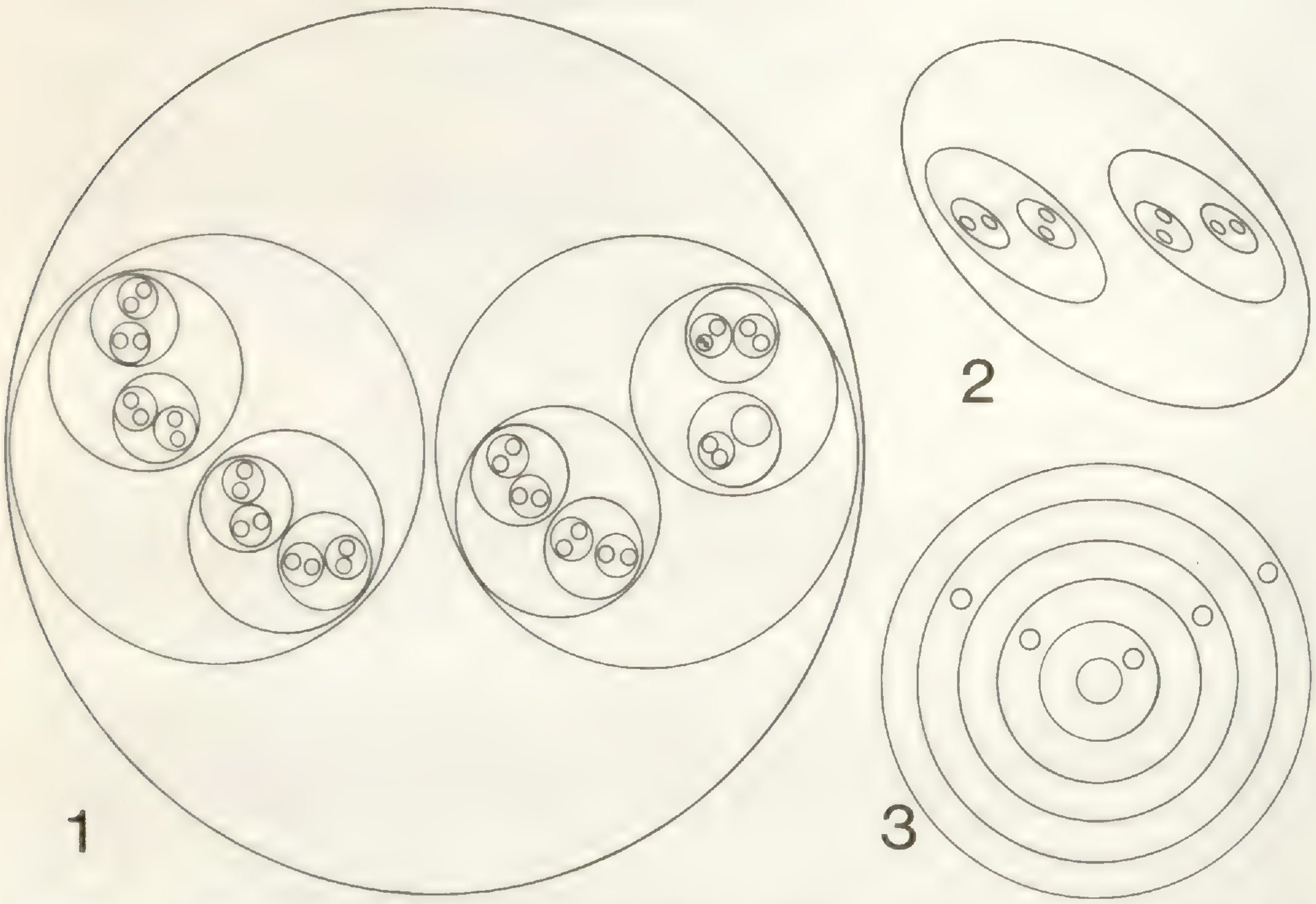
The orientation of successive branchings in a small whole plant of the terrestrial *L. selago* is illustrated diagrammatically in *Fig. 1*. The diagram indicates that most branchings occur in planes inclinate to the preceding branching plane. Cruciate sequences are frequent, mostly in the younger parts, but they hardly ever occur in both branches of a pair; one usually is inclinate and the other perpendicular to the preceding branching plane. In the living plants, the branches usually are more or less ascending, and the inclination of branching planes tends to result in a concentric and concave arrangement of branches, like portions of funnels inserted into each other. Such an arrangement probably catches light more effectively than regular cruciate branch systems would. The orientation of successive branching planes is variable in detail, but in all Ecuadorean species of subg. *Urostachya* it generally corresponds to the pattern found in *L. selago*.

Fresh material of *L. nummulariifolium*, a species which was described by Troll (1937, p. 476, fig. 36611) as flabellate, was found not to be so. It has both flabellate and cruciate sequences (*Fig. 2*). The flattening plane of the whole shoot is due to leaf orientation and does not coincide with the branching planes. In the diagram, the longest diameter of the ellipses indicates the leaf plane.

In most species of subg. *Urostachya*, the branches develop identically, usually with minor variations of length. In the *L. phlegmaria* group, the position of branch contraction (change from expanded leaves to reduced, clasping, and appressed

leaves) is variable in individual branches. The contracted branches in this group are very frequently termed strobili, and the leaves sporophylls. This usage is largely inadequate, as the constricted branches usually are only partially sporangiferous. Furthermore, sporangia often are found in the axils of expanded leaves.

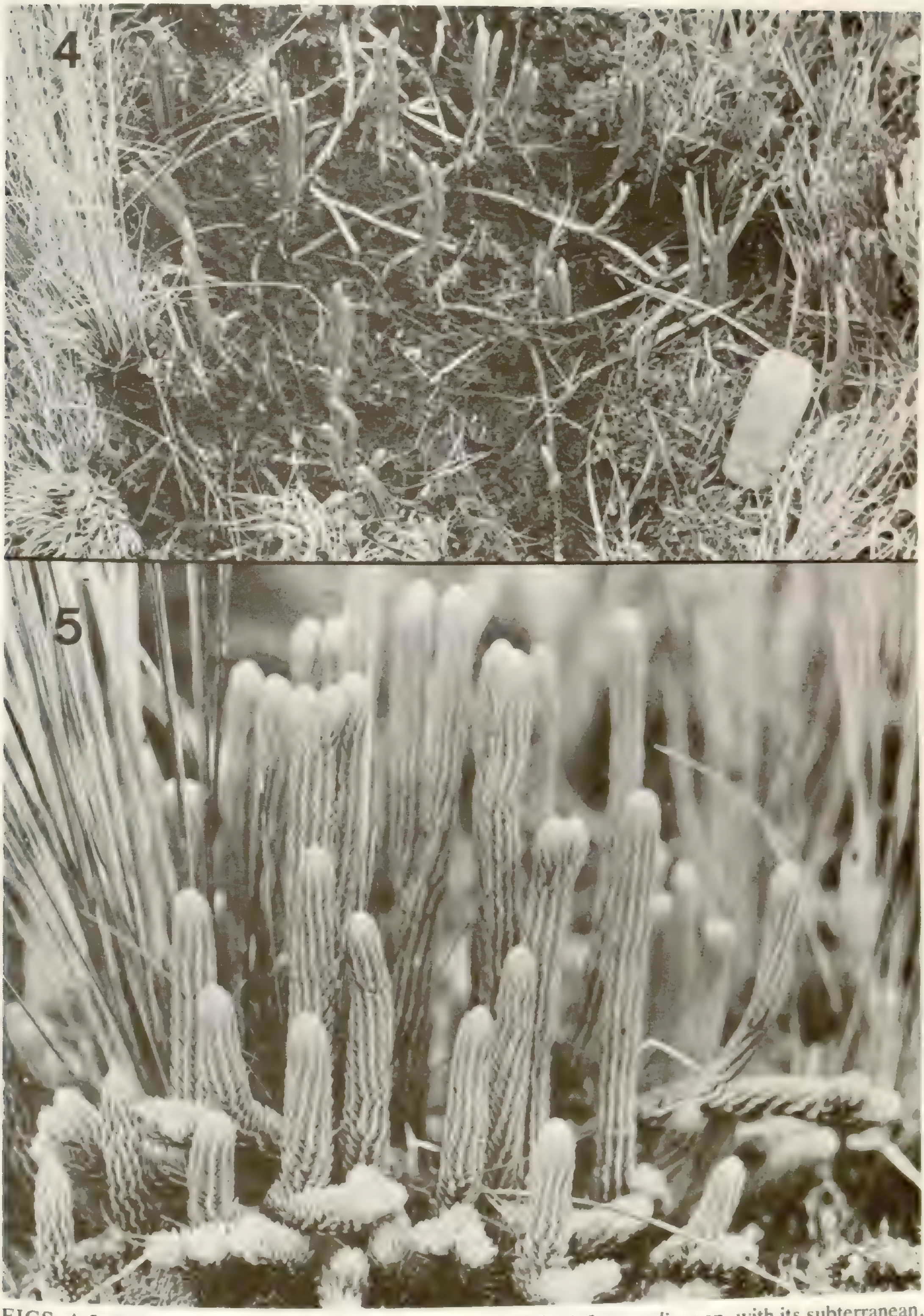
The *L. saururus* group, most of which are high-Andean species, has differentiation of the branches resulting in the development of horizontal rhizomatous and erect aerial branches (*Fig. 5*). The rhizomatous branches produce roots along



FIGS. 1–3. Branching patterns in *Lycopodium*. FIG. 1. Orientation of successive branchings of a whole plant of *L. selago*. Godhavn. Greenland, *Laegaard s.n.* (AAU). FIG. 2. Orientation of successive branchings of *L. nummularifolium*. The longest diamater of the ellipses indicates the shoot flattening plane. New Hebrides, *Braithwaite s.n.* cult. Kew. FIG. 3. Generalized diagram of the rhizome branching in subg. *Lycopodium*.

their underside and may be either superficial or subterranean. In a common yet undescribed species from Ecuador, the production of elongate, subterranean rhizomatous branches enables it to form relatively large clones and to be rather successful in the lower páramo bogs (*Fig. 4*). Apparently this type of branch differentiation does not represent a stable character in all the species in which it occurs; in some of them it is occasional or even rare.

Adventitious shoots may be formed by lateral branching at the base of senile or damaged plants in some terrestrial or epiphytic species, and so may rejuvenate them.



FIGS. 4–5. Habit of species in the *L. crassum* group. FIG. 4. *Lycopodium* sp. with its subterranean, rhizomatous branches uncovered. Páramo de Tufino, Pcia. Carchi, Ecuador. *Øllgaard & Balslev 8517* (AAU). FIG. 5. *L. crassum s. l.* Páramo de Tufino, Pcia. Carchi, Ecuador, *Øllgaard & Balslev 8378* (AAU).

SUBGENUS LYCOPODIELLA

This subgenus includes about 40 species, all terrestrial. They can be divided into three groups discussed below on the basis of habit, including branching pattern. In contrast to subg. *Urostachya*, the species are all basically anisotomous.

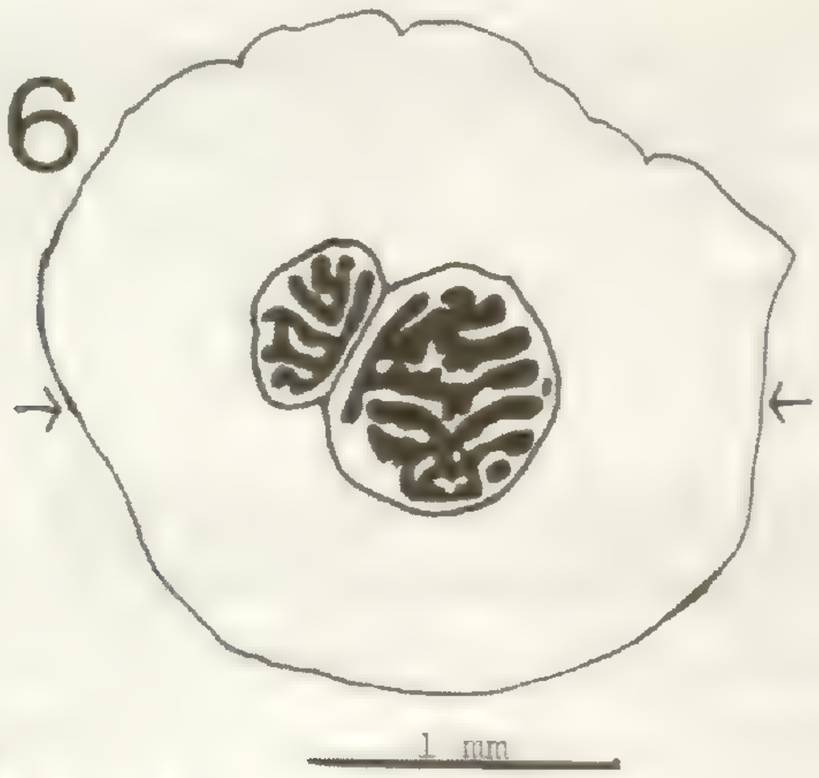
Group of L. inundatum and L. carolinianum.—In fertile plants, the first branching from previously dormant buds of *L. inundatum* L. takes place in the vertical plane and produces an erect, strobilus-bearing branch and a creeping and rooting vegetative branch (*Fig. 8*). Sterile individuals branch only in the horizontal plane. The erect branch usually remains simple, but approximately isotomous branchings may occur as abnormalities. In the large Brasilian plant here tentatively named *L. alopecuroides* var. *furcatum* Fée, the erect branch normally is up to three times branched (*Fig. 7*). The orientation of these branchings is unknown. In several species, the creeping branch may produce up to several erect, strobilus-bearing branches by branching in the vertical plane, whereas all branchings in the horizontal plane result in the formation of creeping, vegetative branches. No inclinate branchings have been found in this group.

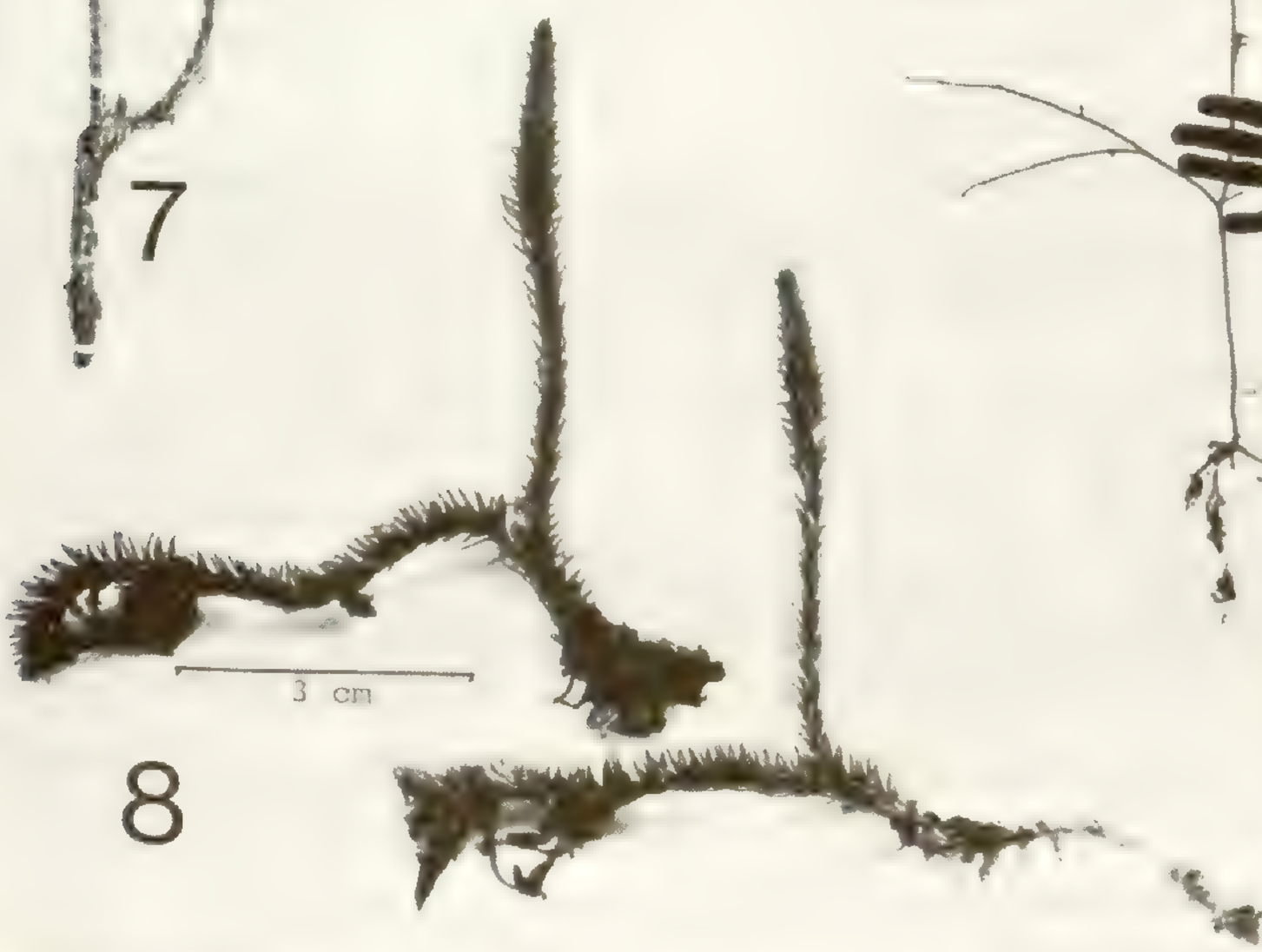
Group of L. cernuum.—This group consists of profusely branched plants, some of which are reminiscent of small Christmas trees. Although they have a common basic pattern, their branching patterns are exceedingly variable, even within one species. The widespread *L. cernuum* L. can serve as a model for the group (*Fig. 11*). Young plants of this species produce an arching or looping main stem that roots upon soil contact and forms a new loop. This may be repeated until the plant is sufficiently strong to branch in the vertical plane, producing an erect branch on the upper side of the loop and a continuing looping branch. In theory, this may continue indefinitely.

The branching pattern of the erect branch of *L. cernuum* was excellently described by Troll (1937, pp. 477–478). The erect branch has a distinct pseudomonopodial main axis which may bear a few arrested buds below the subopposite pairs of horizontal flabellate branchlet systems. The pairs of branchlet systems alternate regularly by ca. 90°, creating an illusion of decussate arrangement. The branch pairs arise by two anisotomies in rapid succession in approximately the same plane. This characteristic difference of branching interval length in the main axis is gradually lost towards the apex of the erect branch. The flabellate branchlet systems ultimately may form small, drooping strobili.

In addition to the erect branches just described, the continuous looping stems produce flabellate anisotomous branchlet systems in the horizontal plane, and sometimes divide nearly isotomously, thus forming a new continuing looping stem. Sometimes the branchlet systems borne on the looping stem may form a few strobili. Sometimes one or two of the lowest branchlets on the erect branch, which mostly remain as arrested buds, develop into new looping stems.

Other taxa of the group differ from *L. cernuum* in branching pattern, mainly with respect to the length of the looping branches and the compoundness and branching sequence of the erect branch.





FIGS. 6–11. Branching in *Lycopodium*. Rhizome branching in *L. complanatum*. The xylem is black; lateral marks indicate the horizontal plane. Pcia. Loja, Ecuador, *Øllgaard s. n.* (AAU). FIG. 7. *L. alopecuroides* var. *furcatum*. São Paulo, Brazil, *Brade 5131* (S). FIG. 8. *L. inundatum*. Gjerrild Nordstrand, Denmark, *Øllgaard s. n.* (AAU). FIG. 9. Subterranean lateral branching in *L. laterale*. New Zealand, *Given 8837* (AAU). FIG. 10. Aerial branching in *L. laterale*. Charleston, W. Nelson, New Zealand, *Wardle s. n.* (AAU). FIG. 11. *L. cernuum*. Above Balzapamba, Pcia. Bolivar, Ecuador. Øllgaard photo.

Group of L. laterale.—This small group is found mainly in Australia and New Zealand. I have had access only to material of *L. ramulosum* Kirk and *L. laterale*. The branching pattern of *L. ramulosum* strongly resembles that of *L. inundatum*, one difference being that the erect, strobiliferous branch is not produced at the first branching, but follows after a sequence of nearly isotomous, horizontal, and flabellate branchings of vegetative stems. I have seen no subterranean parts of this species.

Holloway (1916, p. 255) described the subterranean branching of *L. laterale* (*Fig. 10*) by saying that "The adult plant consists of an irregular and much branched colourless rhizome, which ramifies through the soil in all directions. The shorter branches emerge at the surface to form the erect aerial shoots." The fresh sterile material I have studied of this species has subterranean, ascending rhizomatous stems which branch a few times nearly isotomously in the horizontal plane when they emerge on the surface, almost like in *L. ramulosum*. No further dichotomous development was found in the sterile material. However, the subterranean branching indicated by Holloway is due to true lateral branching. Lateral branches and dichotomous ones as well are formed from superficial and subterranean stems. In the subterranean stems, they usually arise from the undersides of stems in a way and position comparable to roots, breaking through the stem cortex (*Fig. 9*). The anatomy of these branchings remains to be studied more closely. In this connection, it is interesting to note Holloway's (1916, p. 299) remark that "The more deeply growing almost naked rhizome of *L. ramulosum* is interesting as suggesting an intermediate form between the typical scaly rhizome and the leafless adventitious root." The secondary branches may behave like the primary branch, giving rise to tertiary branches, etc.

Erect, strobilus-bearing shoots arise similarly, but ascend more steeply to the surface. Their initial aerial development resembles that of sterile shoots, being flabellate and nearly isotomous. However, after a few dichotomies, orientation of the branching planes becomes irregular. Only two herbarium specimens have been boiled for examination of this character. They gave no idea of a fixed sequence (*Fig. 10*). Strobilar branches apparently originate in almost any position, and thus no definite branching plane was found in which strobili arise, as seems to be the case for the *L. inundatum* and *L. carolinianum* groups and for *L. ramulosum*.

The strobili of *L. laterale* are not lateral in origin as commonly described and indicated by the specific epithet. They are completely differentiated dichotomous branches, or the basal part of the branch may bear normal leaves.

SUBGENUS LYCOPODIUM

This subgenus includes perhaps 60 species which are all terrestrial with subterranean or superficial, creeping, scandent, or climbing pseudomonopodial main stems here termed rhizomes. Wilce (1972) arranged these species in seven groups, some of which are treated as genera by Holub (1975), Löve, Löve and Pichi Sermolli (1977), and Pichi Sermolli (1977).

The basic branching pattern of the groups is very uniform. All species are anisotomous or occasionally isotomous in their rhizome branching. In *L. spurium* Willd., isotomy occurs with fairly regular intervals in the rhizomes, although anisotomy is the prevalent mode of branching. In other species, isotomy seems to occur more randomly. The result of anisotomy is the production of a pseudomonopodial rhizome that gives off minor branches alternately to the left and right.

The orientation of the branching planes in the rhizome is inclinate throughout the subgenus, although my material of *L. casuarinoides* Spring did not show this character with certainty; it had very shallow inclination angles or possibly flabellate branching. The minor branches of the rhizome develop into variously differentiated shoot systems. A main axis may become more or less distinct and bear branchlet systems which in turn may produce strobili. The orientation of branching planes in these shoot systems is invariably inclinate, although the inclination angle is variable, even within the same plant. Frequently it is impossible to determine the inclination angle exactly, particularly in the species with radial branch symmetry. In major branches, the plectostele provides help in discerning the inclination angle of successive branchings, as the orientation of the stelar plates is fairly constant throughout a branching interval, and the stelar plates in derived branch steles are tilted towards each other (*Fig. 6*). In minor branches, the stelar patterns are not helpful for orientation because the steles are radially symmetrical. The effect of inclinate branching of branchlet systems is particularly well displayed in some species of the *L. complanatum* group in which the upper sides of the flattened or quadrangular branchlets are tilted towards each other, although sometimes only slightly so. In some species (e.g., *L. tristachyum* Pursh), the regular inclination of all branchings of the branchlet systems creates a more or less complete funnel-shaped arrangement of branchlets, whereas in other species (e.g., *L. complanatum* L.) the branchlet systems are often flat because the branches bend backwards after their inclinate origin.

DISCUSSION

The main conclusion of the present study is that three types of branching patterns can be distinguished in *Lycopodium sensu lato*, besides the deviating pattern of *L. laterale*, which is incompletely understood. Apart from the latter species, there seems to be perfect correlation of branching pattern types and the subgenera proposed by Wilce (1972), and thus the branching patterns give further evidence for the distinctness of these subgenera.

The distinction between groups which branch isotomously and anisotomously was made long ago. It was one of the basic characters separating Pritzel's subgenera *Urostachya* and *Rhopalostachya*. The existence of distinct branching types in the latter subgenus and the usefulness of branching pattern as a subgeneric character have not been recognized previously. Also, the observation of true lateral branching in *L. laterale* and in some species of subg. *Urostachya* is new.

Troll (1937, p. 474ff.) supported a theory of correlation of shoot symmetry and the orientation of successive branching planes. He claimed that branching in

lycopsids is of two basic kinds, cruciate and flabellate. According to this theory, cruciate branching is correlated with radial symmetry and flabellate branching is correlated with bilateral or dorsiventral symmetry. As examples of the former, he mentioned *L. selago* and other species of subg. *Urostachya*. *Lycopodium nummularifolium* was mentioned as the striking exception in this subgenus; it exhibits correlation of flattened shoots (due to leaf orientation) and flabellate branching pattern. The shoot systems of *L. clavatum* L. and *L. annotinum* L. were claimed to be dorsiventral, even if superficially they appeared to have radial symmetry, and the shoot systems were said to be flabellate. The apparent radial symmetry of the rhizome of *L. complanatum* L. (in correlation with Goebel's observation that in this species branchings do not take place in one plane) was used to support the theory, considering that the aerial branchlet systems of the same species are flabellate and dorsiventral.

The results of the present study contradict Troll's theory of correlations. The arguments against it are as follows. (1) Branching in *L. selago* and its allies was not in any case found to be entirely cruciate. The majority of branchings are inclinate, while some apparently are cruciate, and a few are flabellate. (2) In *L. nummularifolium*, branchings are partly flabellate, but also can be cruciate. When they are flabellate, the branching plane does not coincide with the flattening plane of the leafy shoot (*Fig. 2*). (3) Whether or not the shoots of *L. clavatum* and *L. annotinum* are "truly" radial or dorsiventral, the branching (*Fig. 3*) is inclinate to sometimes indistinctly cruciate. This applies also to all portions of *L. complanatum* plants. While a correlation of shoot symmetry with type of branching orientation seems absent, the flattening of dorsiventral branchlets in the anisotomous subgenera does reflect the branching orientation.

The significance of orientation of successive branchings seems to be different in the infrageneric groups. In subg. *Urostachya*, a rigid, predictable type of sequence has not been discovered. Further studies are needed to determine if a general type or several types exist, or whether this character is determined by ecophysiological factors.

Subgenus *Lycopodium* seems to be uniform in its inclinate-cruciate branchings. The inclination angle is variable, even within a single specimen. Occasionally it can be 90°, and in this case should be termed cruciate. In subg. *Lycopodiella*, at least some cruciate branchings initiate the production of branches with different functions, but a similar consequence is not found in subg. *Lycopodium*. The change from inclinate to cruciate in the latter subgenus is part of a continuously variable character, and only the descriptive terms used have rigid definitions. The branching type of *L. casuarinoides* has not yet been determined because of inadequate material.

Subgenus *Lycopodiella* has anisotomy in common with subg. *Lycopodium*, but in contrast is flabellate in the horizontal plane in looping branches, with a perpendicular branching plane in which originate the fertile branches of *L. inundatum*, *L. carolinianum* L., and their relatives, and in the *L. cernuum* group the erect and ultimately fertile branches. The rather fixed pattern of purely flabellate and cruciate branching sequences is here interpreted as a distinct subgeneric character.

Lycopodium laterale and the closely related *L. ramulosum* pose a puzzling problem. Whereas *L. ramulosum* seems to have a definite, predictable pattern, *L. laterale* is highly irregular. The growth habit of *L. ramulosum* and sterile creeping shoots of *L. laterale* are rather similar, and so are the branching patterns. This points to the assumption that the irregular branching of the fertile shoot system in *L. laterale* is due to its erect position. In contrast, the flabellate pattern of *L. ramulosum* and sterile prostrate branches of *L. laterale* might be due to their prostrate habit. Experiments and further field studies are needed to examine this possible correlation.

In spite of the difference in habit between *L. inundatum* (*Fig. 8*) and *L. cernuum* (*Fig. 11*), there also is a striking similarity. Usually the first unbranched stem formed by the hibernating bud in *L. inundatum* is more or less erect until the first dichotomy, by which the strobilar branch and the creeping branch are formed. This is rather like the first stage of looping stem development in *L. cernuum*. The situation in *L. alopecuroides* var. *furcatum* (*Fig. 7*), in which the "creeping" stem forms a high loop, is even more similar to *L. cernuum*. If the erect branch of *L. cernuum* is reduced to a simple branch, the similarity in habit is striking indeed.

Lycopodium ramulosum could easily be fitted into this common pattern, assuming an essential vegetative development before the formation of strobili. However, its subterranean stems are insufficiently known, and its close alliance with the irregular *L. laterale* makes the homology of its branching pattern with the other groups questionable.

Descriptions of subg. *Urostachya* usually indicate that the roots form a basal tuft. This is the most common situation. However, in the *L. crassum* group, additional roots emerge from the underside of prostrate or subterranean shoots. As indicated above, the distinction between these rooting shoots and erect ones is weak and variable. It is believed that perhaps all species of the subgenus possess the capacity to root as a consequence of soil contact. Internal or cortical roots are produced acropetally at regular intervals in *L. pithyoides* Schlecht. & Cham., according to Stokey (1907). Under certain circumstances, the roots may emerge and penetrate the substrate, instead of penetrating the cortex to the stem base. This capacity is used for vegetative propagation of pendant epiphytic lycopodiums in greenhouse cultivation. Unfortunately, Pritzel's figure 372 (1900, p. 593) of *L. saururus* Lam., which belongs to the same group as *L. crassum* Humb. & Bonpl. ex Willd., does not show the typical growth habit of the species, with short prostrate branches from which the erect elongated branches originate.

The present results do not suggest a rational way to divide subg. *Urostachya*. On the basis of leaf habit, chromosome number, and gametophyte morphology, two or three major groups usually have been recognized (Boivin, 1950; Herter, 1949–1950; Löve, Löve & Pichi Sermolli, 1977; Rothmaler, 1944; Walton & Alston, 1938). The two spore morphologies (Wilce, 1972) do not coincide with these major groups. Heterophylly and homophylly per se are not distinct characters for separation, since many species are intermediate. In addition, some groups which I interpret as natural ones contain both leaf types. Accurate chromosome numbers and gametophytes are known for approximately ten species of a group

totalling perhaps 400 species. Although these characters suggest the existence of more than one group, much more detailed knowledge is necessary before formal recognition at any level is advisable.

Subgenus *Lycopodiella* can be divided into four groups that are based on differences of growth habit, sporophyll and sporangium shape, mucilage canal distribution, spore morphology and chromosome number. Branching patterns indicate three related groups, but the pattern in *L. laterale* does not conform with the basic pattern that is otherwise characteristic of the subgenus. The *L. inundatum* and *L. carolinianum* groups have a very similar branching pattern, but seem distinct on other grounds (Bruce, 1976c). Chromosome numbers are not known for the *L. laterale* group, but otherwise point to distinct numbers for the *L. inundatum* and *L. carolinianum* groups, whereas in the *L. cernuum* group, several odd counts make it impossible to deduce the base number unambiguously. Despite the aberrant branching of *L. laterale*, there is hardly reason to doubt that it is more closely related to the species of subg. *Lycopodiella* than to any other group.

In subg. *Lycopodium*, Wilce (1972) informally recognized seven groups. Some of these are treated as genera by Holub (1975) and Pichi Sermolli (1977). Although the branching patterns of this group are very uniform, other characters are not. Six spore types, five leaf habit types, and four doubtfully distinct types of sporangium wall structure are known from the seven groups. Two gametophyte types are represented in the five groups that have been studied. Different chromosome numbers are recorded from four of the groups. These discontinuities coincide to a great extent with the group limits and contribute to the distinction of separate evolutionary units in the subgenus. On the other hand, the same characters are mainly variations of common basic characters which are distinct from those of the other subgenera. It is therefore doubtful that these groups are sufficiently distinct to be given higher than sectional rank.

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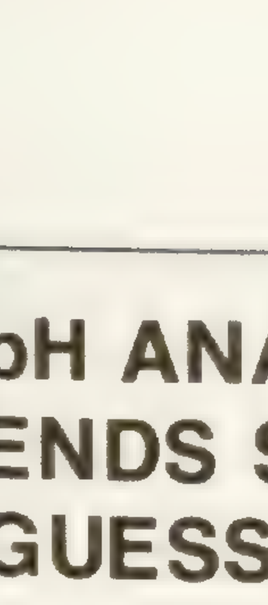

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SHORTER NOTES

ISOËTES BUTLERI IN GEORGIA. — Recently, Baskin and Baskin (Amer. Fern J. 68:7–8. 1978) reported stations for *Isoëtes butleri* Englem. from Kentucky, Tennessee, and Alabama as representing the known distribution of the species east of the Mississippi River. Since then, we have collected it on 20 Apr 1978 in a cedar glade drained by West Chickamauga Creek in Catoosa County, Georgia, 34°54′20″N and 85°14′48″W (*Boom 63*, TENN). According to J. M. Baskin (pers. comm.), C. L. Boynton (Biltmore Bot. Stud. 1:147. 1902) reported finding *I. butleri* in 1899 in Chickamauga Park, which he incorrectly ascribed to Dade Co., Georgia. It is not clear whether this is a sight report or if specimens were collected, but it is likely that this and our localities are in the same area. Dr. Wilber Duncan (pers. comm.) does not record its existence in the state. We believe our collection represents a southeastern extention of the species' range of approximately 120 miles from the cedar glades of the Central Basin of Tennessee, and constitutes the first documented report of its occurrence in Georgia.

The mature megaspores of our specimens lack the distinct or confluent tuberculate ornamentation which is typical of most *I. butleri*, according to Taylor, Mohlenbrock, and Murphy (Amer. Fern J. 65:33–38. 1975), and instead appear rather smooth even when examined at 1300× with the SEM. The taxonomic significance of this character-state appears doubtful, but future collections of additional populations of *I. butleri* from Georgia should be examined in this context. The possibility that smooth megaspores are somehow environmentally induced or geographically related should be tested experimentally.

The plants we collected were from a population restricted to a moist mud depression along a small intermittent stream which drains the limestone glade. Within a month after our collection, the visible population had shrunk considerably in size as the glade began to enter its annual dry season. Therefore, this species should be sought in early spring in the northwestern Georgia counties. Geologically, Georgia is probably best known to botanists for the sediments of the Coastal Plain and the igneous and metamorphic rocks of the Piedmont. The northwestern portion of the state, however, is characterized by Paleozoic rocks of which a considerable portion is limestone. Typical cedar glades tend to develop in areas where this limestone outcrops, creating ideal conditions for the calciphilous *I. butleri*.—*Brian M. Boom* and *A. Murray Evans, Department of Botany, University of Tennessee, Knoxville, TN 37916.*

JUVENILE LEAVES OF THE APOGAMOUS FERN NOTHOLAENA COCHISENSIS.—Cochise's Cloak Fern is a desert or semi-desert dweller which ranges from central and western Texas to California and south into Mexico at least to the state of Aguascalientes. Material of this species from McKelligan Canyon, El Paso, Texas (*Knobloch 2523*, MSC) recently has been proven to be apogamous since no archegonia are present and the sporophyte arises from a single cell layer in back of the sinus (D. P. Whittier, pers. comm.).

In sexual species of ferns, the first leaf arises from an upper part of the embryo, but in *N. cochisensis*, the stem apex arises from a mound of vegetative cells of the prothallus, and all the leaves come from this stem apex.

FIG. 1. Heteroblastic leaf sequence in *N. cochisensis* (*Knobloch 2523*, MSC). × 1.3.

As in most species of ferns, the first leaves of *N. cochisensis* do not resemble the adult ones (*Fig. 1*). Wagner (Amer. J. Bot. 39:578–592. 1952) describes this heteroblastic development in several other species. In *N. cochisensis*, the first leaves are tiny and invariably simple. They vary greatly in shape, much more so than do adult leaves. The first leaves gradually die as they are replaced by younger ones. Depending upon growing conditions perhaps, eventually pinnate leaves appear. Why the genes for pinnateness are repressed in early development is not known, but it seems evident that the extent of photosynthetic leaf surface developed is sufficient for the requirements of the plant at each stage. The first leaves are for the most part devoid of the dense indument that characterizes the adult leaves.—*Irving W. Knobloch, Department of Botany and Plant Pathology, Michigan State University, East Lansing, MI 48823.*

A THELYPTERIS NEW TO FLORIDA.—Over the past two years field studies by Nauman and Austin have turned up two additional species for the flora of the United States, *Pleopeltis revoluta* (Spreng. ex Willd.) A. R. Smith and *Tectaria incisa* Cav., both from Broward County, Florida.

A third species was found in November of 1978, *Thelypteris grandis* A. R. Smith var. *grandis*. Previously this variety was known from the Greater Antilles and St. Kitts in the Lesser Antilles (Smith, Univ. Calif. Publ. Bot. 59:1–143. 1971) and is here recorded as new for the United States. Other varieties of *T. grandis* occur in Central and South America. Voucher specimens have been deposited at the following herbaria: FAU, FLAS, UC, and US.

Thelypteris grandis was discovered by Daniel Austin and me while studying the vegetation of the Fakahatchee Strand portion of the Big Cypress National Preserve. The plants were found growing in a mixed swamp dominated by *Taxodium distichum*. About a dozen individuals formed a single colony on one of a series of tram roads. Essentially limestone spoil mounds, the trams are abandoned access roads from a logging operation in the 1940's and 1950's.

This is the most distinctive species of *Thelypteris* occurring in Florida. It is easily recognized by its large size, with fronds more than 1.5 m long and 0.5 m wide. Other distinctive features include the creeping rhizome, deeply incised pinnae mostly 2–3.5 cm wide, and the costa being uniformly puberulous below. The type variety is distinguished from the other varieties by the greatly reduced basal segments of the pinnae, the glabrous or sparsely hairy indusia, and the nearly medial sori (Smith, loc. cit.).

Whether *T. grandis* is a casual occurrence from the Antilles, native, or an escaped cultigen is at present uncertain; further study may shed more light on this question.—*Clifton E. Nauman, Department of Biological Sciences, Florida Atlantic University, Boca Raton, FL 33431.*

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A New Nephrolepis Hybrid From Florida

CLIFTON E. NAUMAN*

Nephrolepis is a genus of probably 30 species mostly pantropical in distribution. Several species have been problematical in their identification, notably *N. biserrata* (Swartz) Schott, *N. exaltata* (L.) Schott, and *N. hirsutula* (Forst.) Presl (Christensen, 1932, p. 74; Copeland, 1947, p. 91). Two of these species, *N. exaltata* and *N. biserrata*, occur in Florida and have been a source of difficulty, in part because of plants intermediate in a number of characteristics. The intermediates appear to represent hybrid populations between these two species.

Distributional data show that intermediates occur only in the overlapping portions of the parent species' ranges and not where only one parent occurs. Intermediates are found wherever *N. exaltata* and *N. biserrata* occur together, usually in disturbed portions of the habitat. The intermediates are more abundant and luxuriant as would be expected of hybrids.

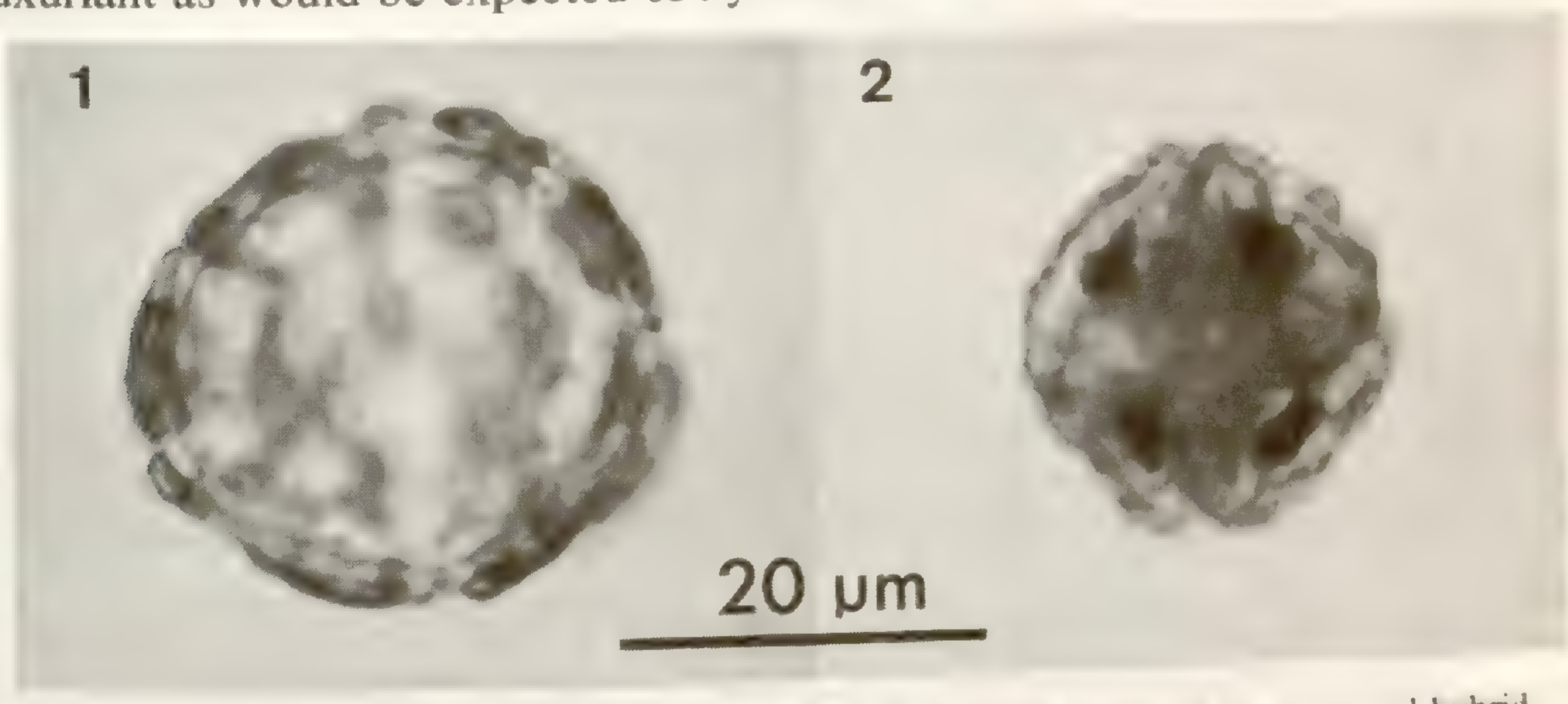

FIG. 1. Spherical spore of the proposed hybrid. FIG. 2. Aborted tetrad of the proposed hybrid.

Cytology does not rule out the possibility of hybrids between *N. biserrata* and *N. exaltata* since both species have been reported to have the same gametic number, $n=41$, (Abraham et al., 1962; Chiarugi, 1960; Fabbri, 1965; Walker, 1964–65, 1973).

Spore morphology provides further evidence of hybridity in the intermediates. *Nephrolepis* is characterized by free, anisopolar, bilateral, monolete spores (e.g., Erdtman & Sorsa, 1971). Spores of the intermediate are irregular, spherical, and alete (*Fig. 1*) and demonstrate features similar to those described by Morzenti (1962) for *Polystichum* hybrids. A large number of aborted spores and aborted tetrads (*Fig. 2*) also are characteristic of these plants. Frequency distributions of spore size are platykurtic when compared to those of the putative parent species (*Fig. 3*). This distribution appears to be a significant feature of fern hybrids (Daigobo, 1967; Kanamori, 1969, 1971; Wagner & Chen, 1965).

*Dept. of Biological Sciences, Florida Atlantic University, Boca Raton, FL 33431.

Volume 69, number 2, of the JOURNAL was issued June 26, 1979.

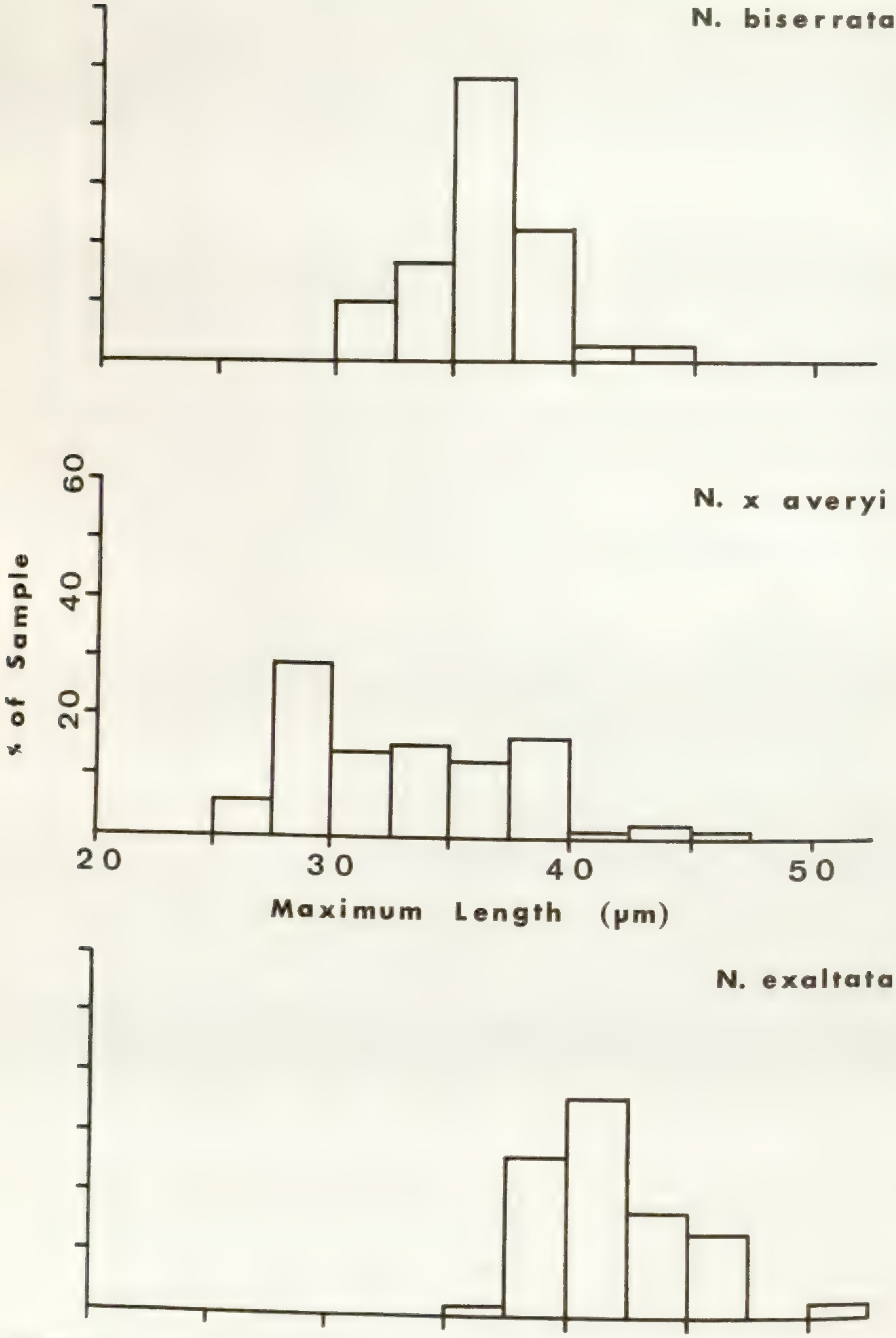

FIG. 3. Frequency distributions of maximum spore length in three of the Florida taxa of *Nephrolepis*.

Morphological intermediacy occurs in several characters, and is demonstrated by polygonal graphs of mean values of eight characters (*Fig. 4*). Scatter diagrams suggest some degree of backcrossing in addition to hybrid intermediacy (*Fig. 5*). In Florida, the adaxial surfaces of the costae of *N. biserrata* typically are tomentose; those of *N. exaltata* are glabrous. The intermediates are slightly pubescent.

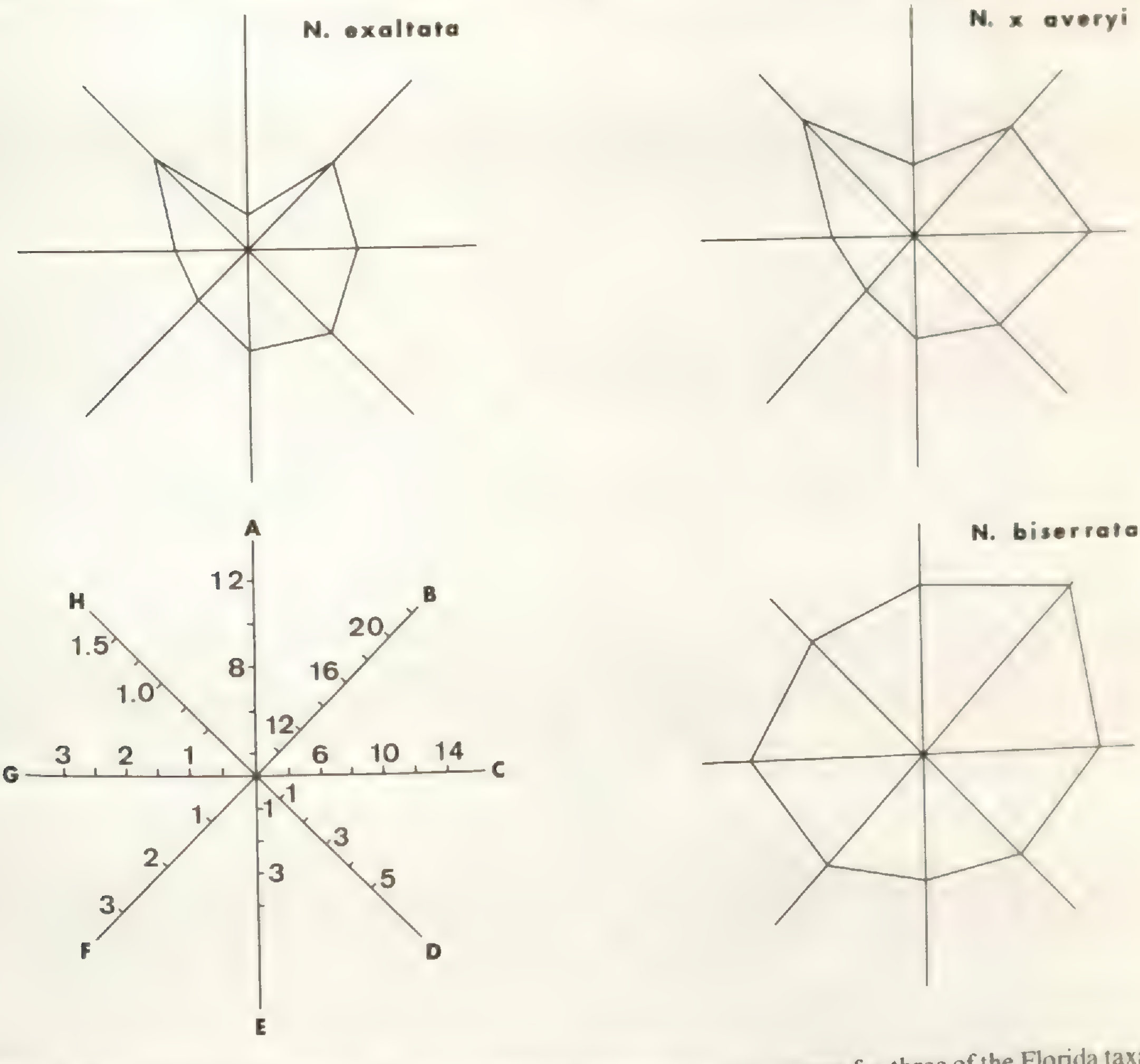

FIG. 4. Polygonal graphs of mean values of eight morphological characters for three of the Florida taxa of *Nephrolepis*. A = Pinna length (cm). B = Interpinna distance (mm). C = Frond length (dm). D = Pinna tip shape (1–5 are coded states from obtuse to narrowly attenuate). E = Acroscopic lobe shape (1–4 are coded states from no lobe to a linear lobe). F = Pinna attachment (1–3 are coded states from sessile to subpetiolulate). G = Lower pinna length/width ratio. H = Pinna width (cm).

Indusium width also is intermediate: in *N. biserrata* about 1.0 mm, in *N. exaltata* about 1.35 mm, and in the intermediates about 1.26 mm. Blade length/width ratios average 9.53 (6.86–17.93) in the intermediates, 5.08 (3.04–7.79) in *N. biserrata*, and 8.40 (4.30–16.98) in *N. exaltata*.

Mixtures of character states also occur in the intermediates. When characters of indusium shape and attachment are examined in typical representatives of *N. biserrata* and *N. exaltata*, the two species are distinct. *Nephrolepis biserrata* has orbicular, peltate indusia, and *N. exaltata* has reniform indusia attached by a point

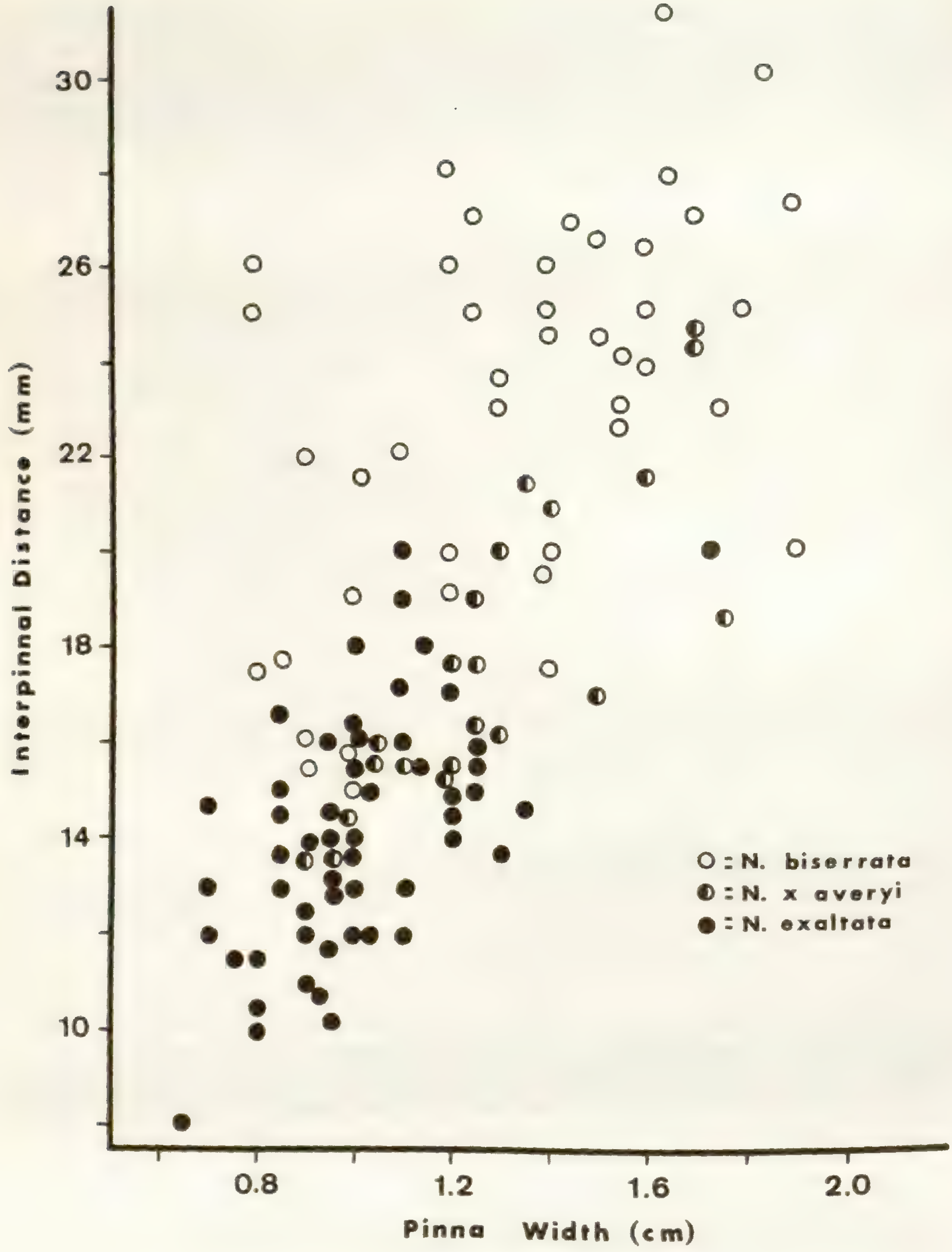

FIG. 5. Scatter diagram of interpinna distance versus pinna width of three of the Florida taxa of *Nephrolepis*.

in the sinus. Occasionally a mixture of indusium types is found on a single plant, apparently always on the intermediates. Pinna shape of the intermediates is falcate like that of *N. exaltata*. Frond length approaches that of *N. biserrata*.

At least two characters suggest hybrid vigor. The stipe length of *N. biserrata* and *N. exaltata* is 2.3 and 1.7 dm, respectively, but in the intermediates it is 2.7 dm. Trichome length in *N. biserrata* is consistently 0.3 mm; in the intermediates it is consistently 0.4 mm.

The morphological intermediacy and spore morphology of the hybrids fulfill two of the three criteria for hybridity given by Wagner and Chen (1965). Distribution and habitat ecology also make hybrid origin of the intermediates likely. The hybrids may be known as:

Nephrolepis × averyi Nauman, hybr. nov.

Planta inter *N. biserratam* et *N. exaltatam* interposita et verosimiliter per hybridionem harum specierum orto. Costae abaxiales leviter pubescentes. Indusia orbicularia vel reniformia, peltata vel in sinu affixa. Sporae abnormales et abortivae, sphericae, diametro 32.6 μm.

Epiphytic, epipetric, or terrestrial plants with fronds up to 3.0 m long. Stipes 1.0–5.25 dm long, glabrous, paleate with lanceolate-attenuate, brown scales. Rachises 0.5–2.6 m long, paleate, otherwise glabrous. Pinnae falcate, 3.6–8.0 cm long and 1.0–1.75 cm wide, truncate to truncate-auriculate at the base, narrowly acute at the tip, with serrulate margins, costae abaxially lightly pubescent, lamina adaxially and abaxially glabrous to occasionally pubescent and lightly paleate. Sori intramarginal to supramedial. Indusia orbicular to reniform, peltate to attached in the sinus. Annulus with 13 or 14 indurated cells. Spores abnormal and abortive, spherical, 32.6 μm in diameter.

TYPE: Fakahatchee Strand off West Grade, 50 ft E of Indian Mound Slough Bridge, Collier Co., Florida, 29 Jan 1979, *Nauman et al. 635* (US; isotypes FAU, FLAS, GH, MSC, NY).

Associated with its parents *N. biserrata* and *N. exaltata* in hammocks and swamps. Distributed in southern Florida (Broward, Collier, Dade, Palm Beach and Pinellas Counties, and probably others). Named after George N. Avery.

The hybrid is best distinguished from *N. exaltata* by its larger size and lightly pubescent upper costal surfaces, and from *N. biserrata* by its falcate pinnae, and narrower fronds.

PARATYPES (all from Broward Co., Florida): Cypress Creek Hammock, Nov 1976, *Durand 65* (UC), *Durand 71* (FSU), 12 Oct 1978, *Nauman 434* (TENN), *Nauman 436* (USF).

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REVIEW

"THE PTERIDOPHYTES OF SURINAME," by K. U. Kramer. Natuurw. Stud. Suriname Ned. Antill. 93:1–198. 1978.—In format this work is essentially a second edition of Posthumus' "Fern Flora of Suriname" (1928). But it is much revised, corrected, and expanded over its predecessor. Considerable collections have been made in Suriname over the past fifty years, especially in the mountainous central portion that is underlain by Roraima sandstones. This area has floristic affinities with Guayana and southern Venezuela, and so contains many species not recorded by Posthumus.

Kramer's treatment includes 334 taxa of ferns and fern-allies in 63 genera. For the most part, the genera are conservatively and broadly delimited, a course chosen by the author because of the lack of definitive knowledge in splitting such genera. The work contains a very novel and useful multiple-entry key to most genera (a few are treated in a conventional key). By scoring an unknown specimen for up to eight characters, a unique or nearly unique profile results that can be matched against a list of characters for each genus. Those who have worked with incomplete material will appreciate this approach over a conventional key.

The keys to species appear to be accurate and well constructed. Although the Flora lacks descriptions and illustrations, there are few enough taxa, even in the largest genera (*Trichomanes*, 37; *Polypodium*, 30; *Adiantum*, 21), that the keys distinguish them adequately and the chance of arriving at a wrong name is slight. Important literature is given for the Flora as a whole and for each genus. An index showing accepted names and synonyms concludes the volume, which may be purchased for D. fl. 48 (ca. $23.50) from the Foundation for Scientific Research in Suriname and the Netherlands Antilles, Plompetorengracht 9–11, NL-3512 CA Utrecht, Netherlands.—*D.B.L.*

Spore Morphology of Anemia subgenus Anemia

STEVEN R. HILL*

As a continuation of earlier work on the schizaeaceous genus *Anemia* Swartz (Hill, 1977), I have examined spores of nine species of subg. *Anemia* by means of the scanning electron microscope. This subgenus, unlike subg. *Coptophyllum*, which was revised by Mickel (1962), has not been critically treated since the revision of the Schizaeaceae by Prantl (1881). The present work was initiated to help clarify the relationships of some of the species in the subgenus which have vegetative specializations by examining the spores, which are assumed here to have a more conservative rate of change than the vegetative characters.

Spore samples were collected either in the field or from selected herbarium specimens. Twenty-three specimens of the nine species were mounted on aluminum stubs with double-adhesive tape and coated with a thin layer (200–400 Å) of gold-palladium. The prepared samples were then examined at 15 kV and photographed using the JEOL JSM-U3 Scanning Electron Microscope of the Electron Microscopy Center, Texas A&M University. Proximal, distal, and ornamentation detail micrographs have been included in most cases to allow comparison at each orientation. Line scales indicate size based upon instrument magnification readings and are best used to indicate relative size. In the following list of vouchers, collections cited with an asterisk are illustrated in this paper and known herbarium locations for each collection are cited.

Anemia hirsuta (L.) Swartz. **MEXICO: Jalisco:** Ayo el Chico, *McVaugh 17167* (US). **Temascaltepec:** Ixtapan, *Hinton 1640* (US). **Oaxaca:** Juchatengo, *Hill 1643** (NCU, NY, VT); Villa Alta, *Vera-Santos 3517* (US).

Anemia munchii Christ. **MEXICO: Oaxaca:** Dist. Juchitán, 6 km S of Matías Romero, *Hill s.n.** (spore collection only, living material at NY).

Anemia oblongifolia (Cav.) Swartz. Group I (see text). **BRAZIL: Goiás:** Serra dos Pyrenaos, *Anderson, Hill et al. 10296** (NY, UB); Serra Dourada, *Irwin et al. 11793** (NY, UB, US).

Anemia oblongifolia (Cav.) Swartz. Group II (see text). **BRAZIL: Goiás:** Serra dos Cristais, *Irwin et al. 13216a** (NY, UB, US); Serra dos Pyrenaos, *Irwin et al. 10977* (NY, UB, US); Alto Paraíso, *Hill 1036* (VT).

Anemia ouropretana Christ. **BRAZIL: Minas Gerais:** Serra do Espinhaço, *Irwin et al. 27976** (NY, UB, US).

Anemia pastinacaria Moritz. **MEXICO: Guerrero:** Plan del Carrizo, *Hinton 14650* (US). **BRAZIL: Goiás:** Chapada dos Veadeiros, *Irwin et al. 24260* (NY, UB, US); Serra do Caiapó, *Anderson, Hill et al. 9466** (NY, UB).

Anemia phyllitidis (L.) Swartz. **MEXICO: Oaxaca:** San Gabriel, *Hill 1661* (VT). **Chiapas:** El Zapotal, *Laughlin 2563** (US). **BRAZIL: Distrito Federal:** Córrego Landim, *Irwin et al. 11333* (NY, UB, US). **Goiás:** Serra dos Pyrenaos, *Irwin et al. 18947* (NY, UB, US); Serra Dourada, *Hill 1089* (VT). **Minas Gerais,** Serra do Espinhaço, *Anderson, Hill, et al. 9467** (NY, UB).

Anemia pohliana Sturm. **BRAZIL: Goiás:** Jataí, *Chase s.n.** (US).

Anemia radicans Raddi. **BRAZIL:** Espírito Santo: Cachoeiro de Itapemirim, *Foster & Foster 971** (US).

Anemia rotundifolia Schrad. **BRAZIL: Bahía:** Toca de Onca, *Rose & Russell 20099** (NY, US).

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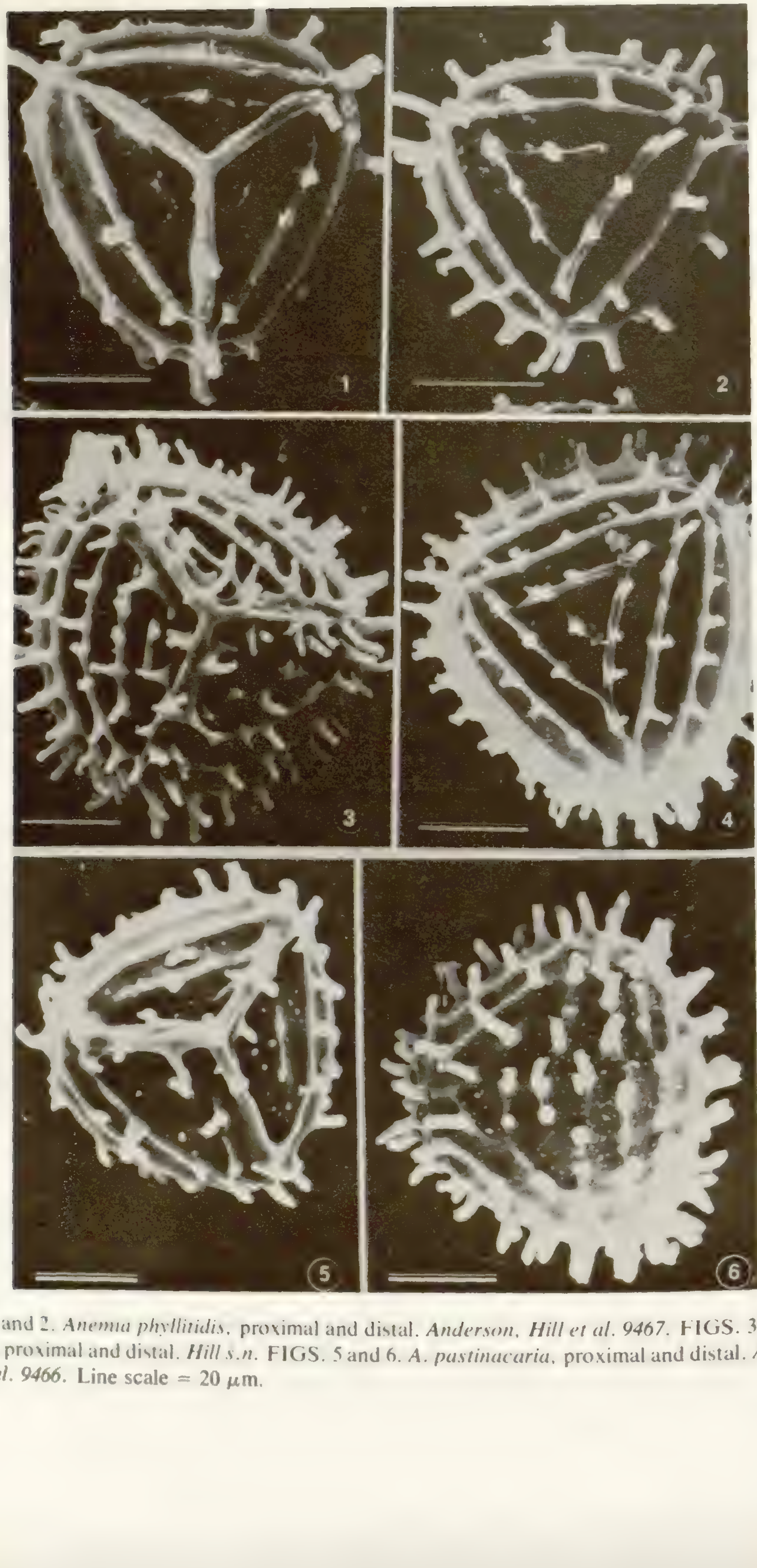
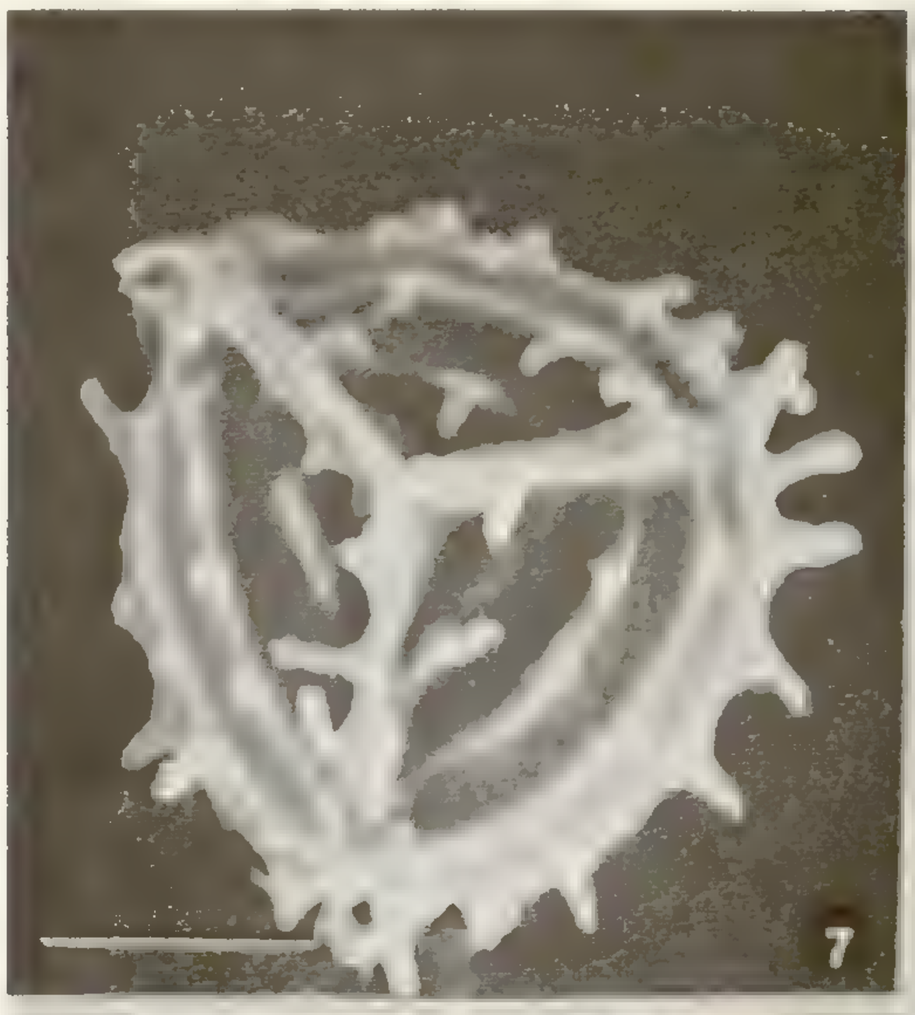
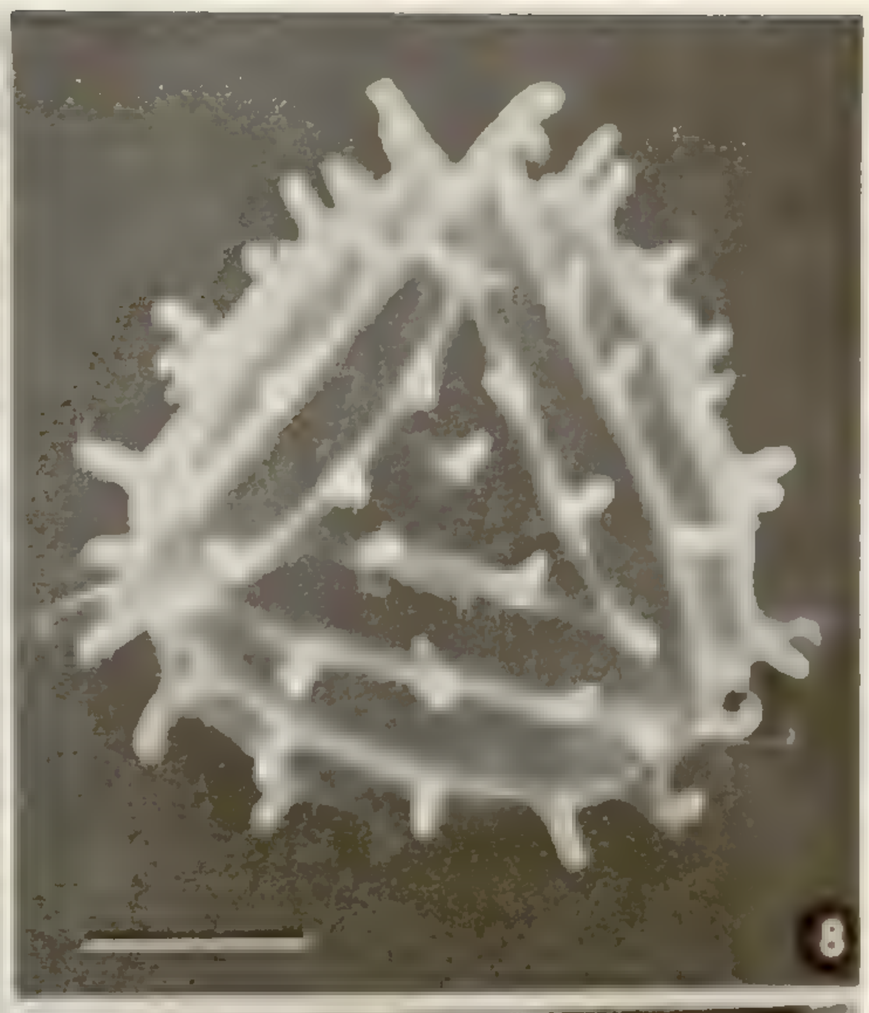
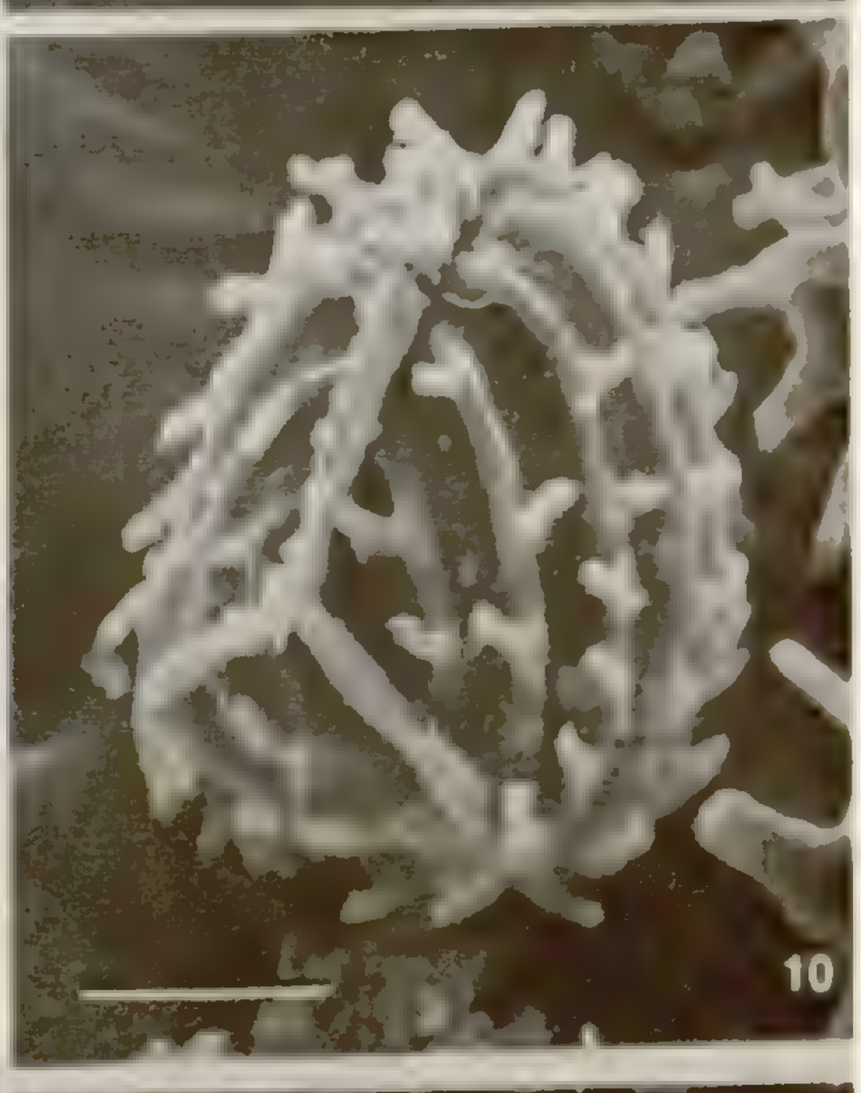
*Department of Biology, Texas A&M University, College Station, TX 77843. Present address: Department of Botany, University of Maryland, College Park, MD 20742.

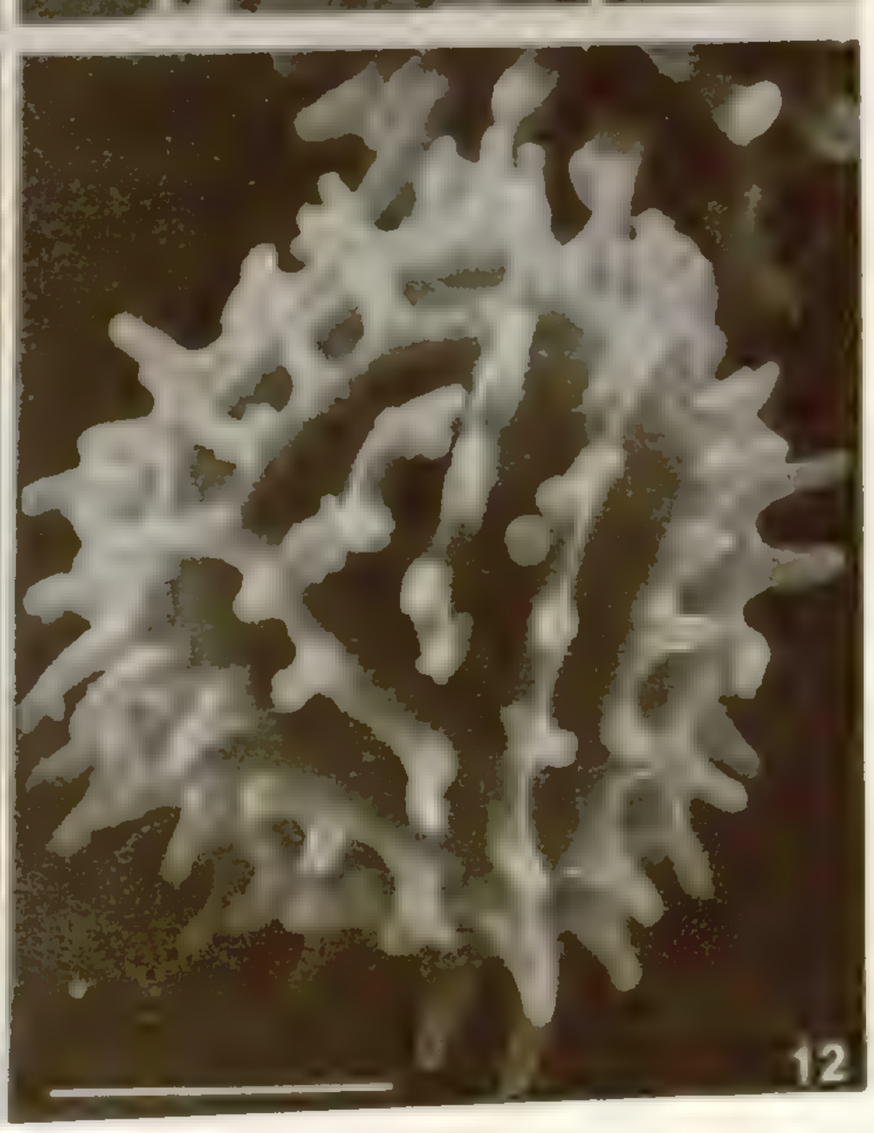


FIGS. 1 and 2. *Anemia phyllitidis*, proximal and distal. *Anderson, Hill et al. 9467.* FIGS. 3 and 4. *A. munchii*, proximal and distal. *Hill s.n.* FIGS. 5 and 6. *A. pastinacaria*, proximal and distal. *Anderson, Hill, et al. 9466.* Line scale = 20 μm.

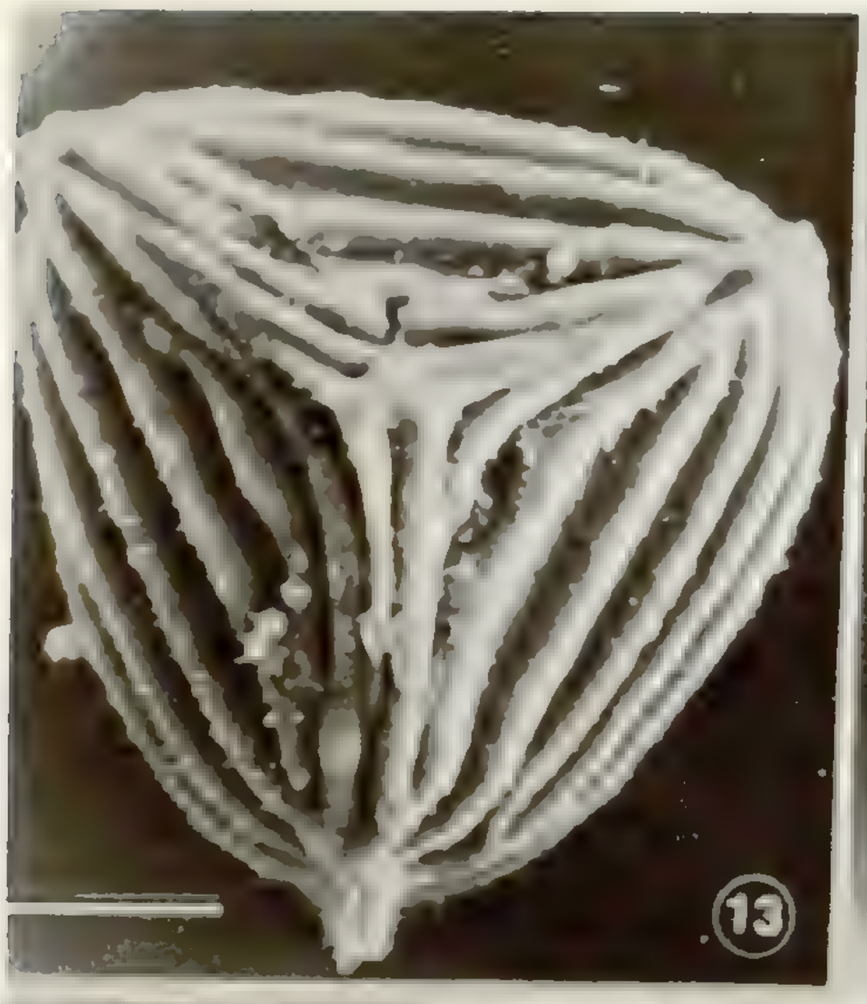


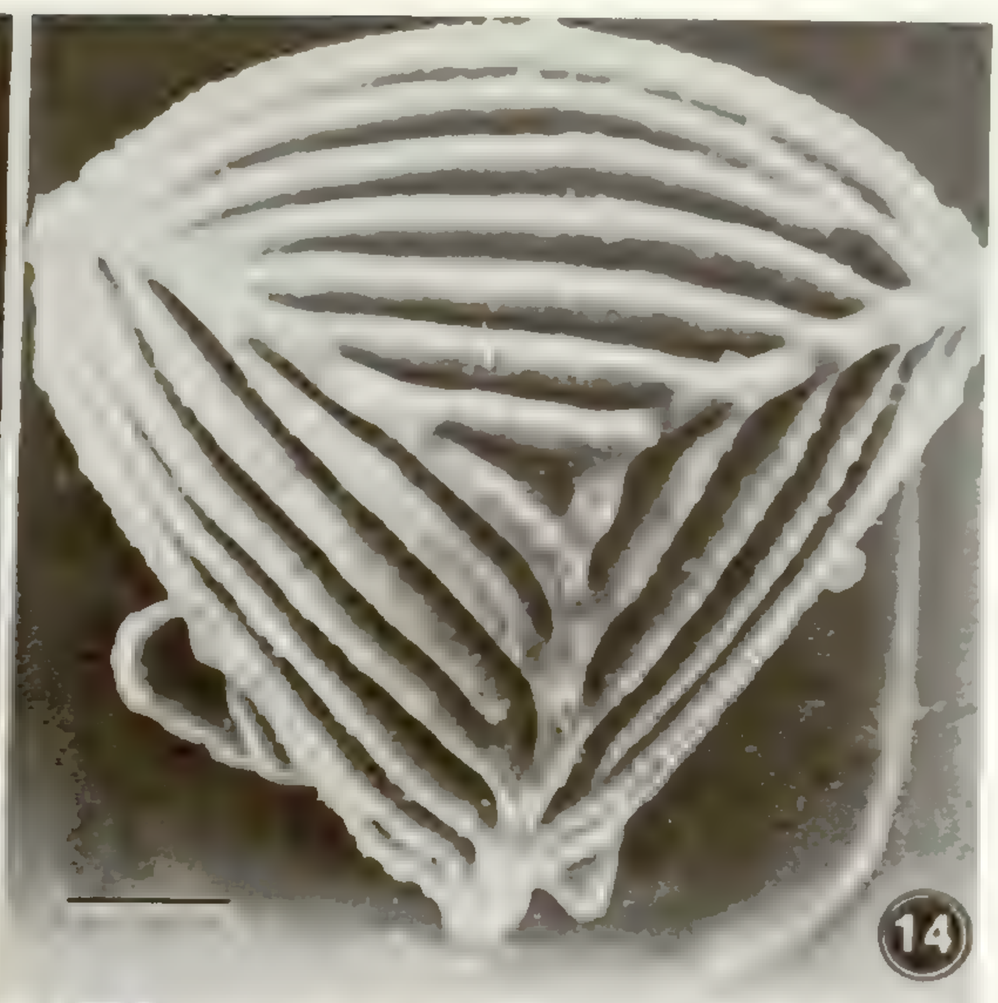


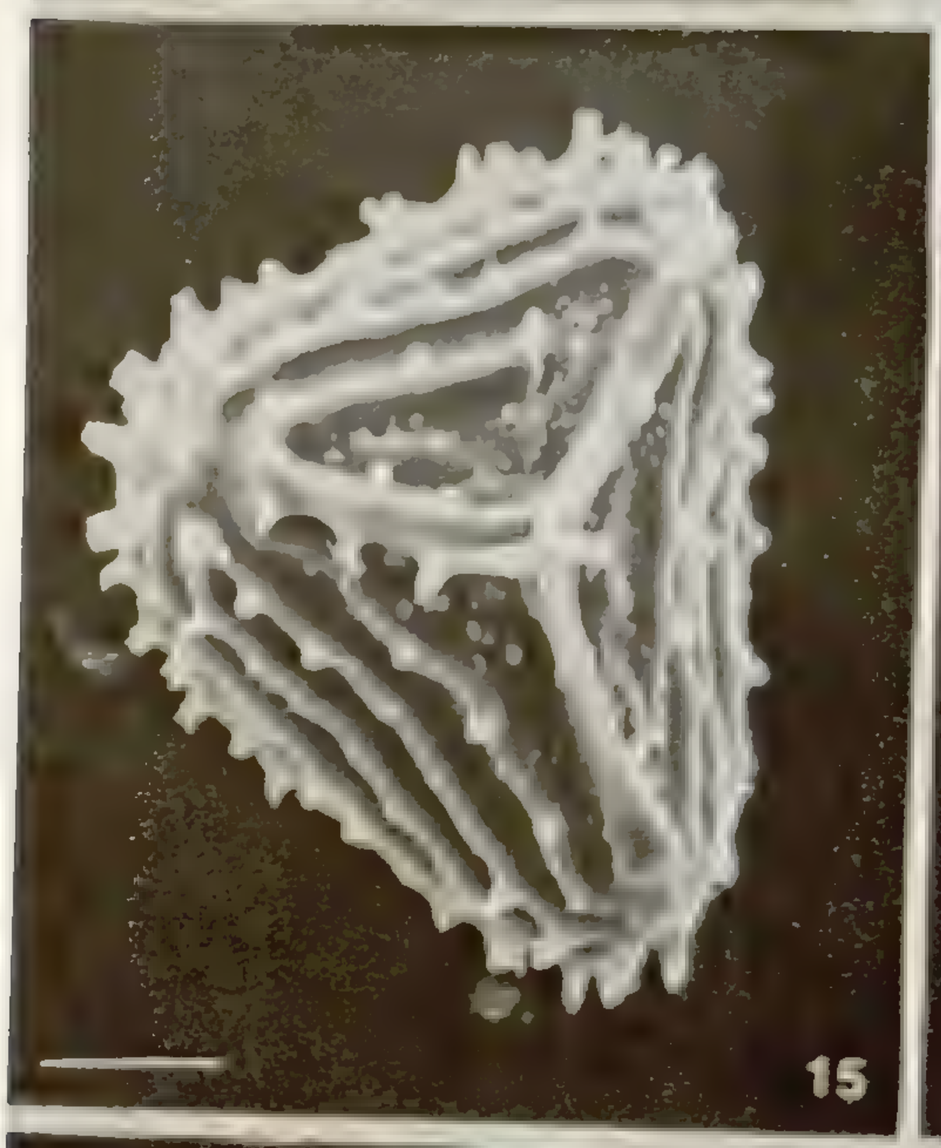


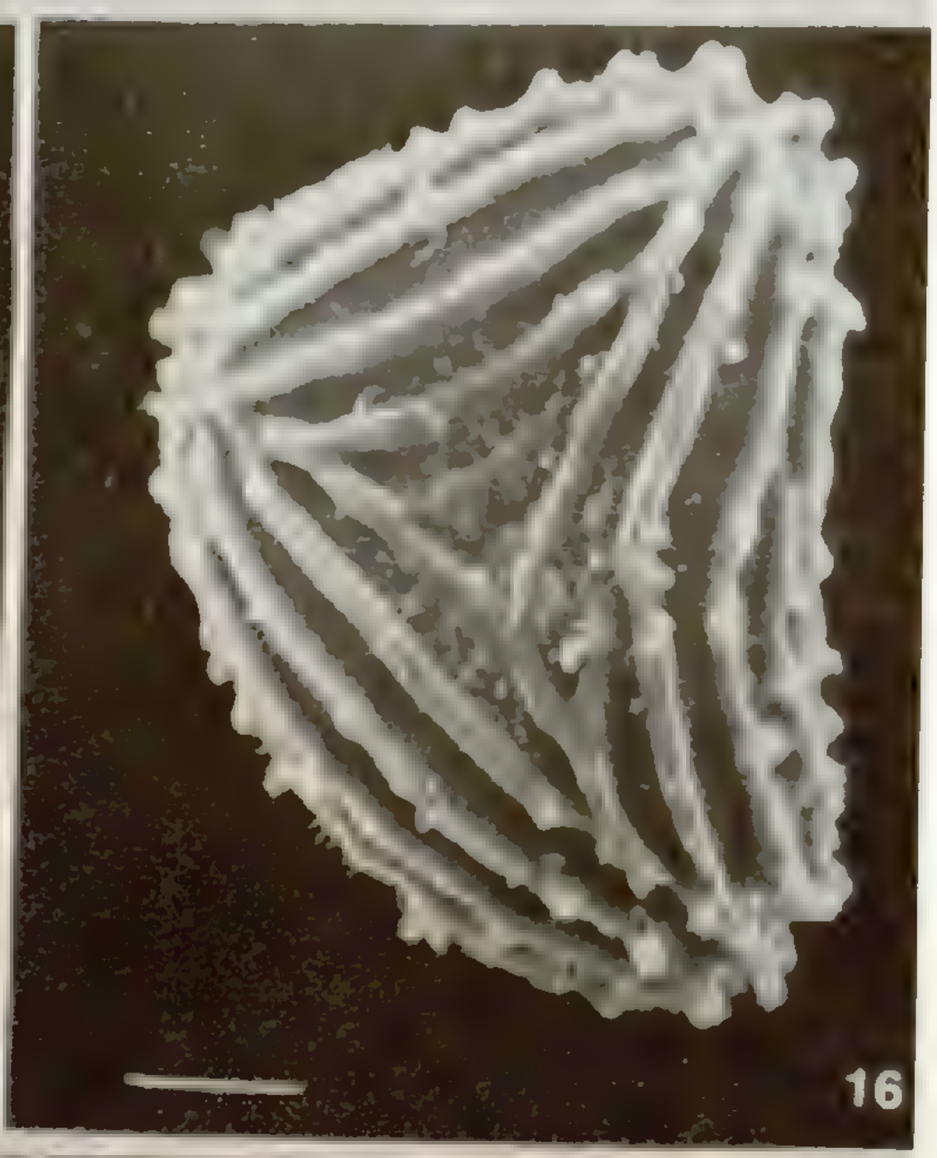


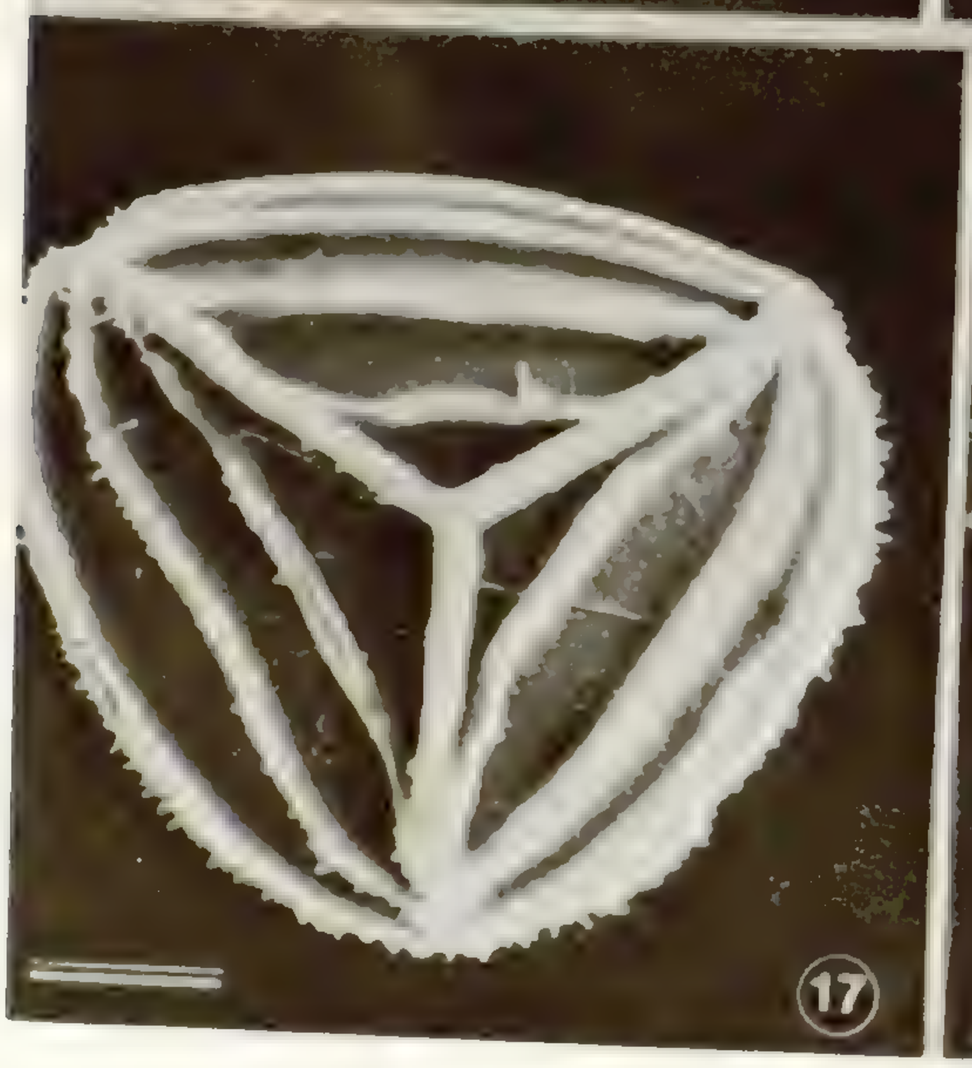
FIGS. 7 and 8. *Anemia ouropretana*, proximal and distal. *Irwin et al. 27976*. FIG. 9. *A. radicans*, proximal. *Foster 971*. FIG. 10. *A. pohliana*, proximo-lateral. *Chase s.n.* FIGS. 11 and 12. *A. rotundifolia*, proximal and distal. *Rose & Russell 20099*. Line scale = 20 μm.











FIGS. 13 and 14. *Anemia oblongifolia*, Group I, proximal and distal, *Anderson, Hill, et al. 10296*. FIGS. 15 and 16. *A. oblongifolia*, Group II, proximal and distal, *Irwin et al. 13216a*. FIGS. 17 and 18. *A. hirsuta*, proximal and distal, *Hill 1643*. Line scale = 20 μm.

RESULTS

With important exceptions to be noted below, the spores of taxa in *Anemia* subg. *Anemia* are tetrahedral with several widely-spaced, narrow ridges on each face separated by smooth unornamented zones. The ridges usually possess large, terete, rod-shaped appendages called baculae.

Spores of *Anemia phyllitidis*, the type species of the genus and of subg. *Anemia* and one of the most widespread species, are illustrated in *Figs. 1, 2,* and *19*. The variable spores are 50–60 μm in diameter exclusive of the baculae. The ridges are typically very narrow and are separated by unornamented zones or furrows (fossulae) 5–10 μm wide. The baculae are 6–10 μm long and truncate, and on the ridges between them are smaller microspines 1–2 μm long.

The spores of *A. munchii*, a narrowly distributed species, differ primarily in their more highly ornamented ridges *(Figs. 3, 4,* and *20)*. The trilete scar has at least three rows of spines, compared with the single row in *A. phyllitidis*, the spores are 10–20 μm larger (60–70 μm) on the average, and tend to be more spherical. The baculae are narrower and the ridges tend to lack the smaller microspines.

Anemia pastinacaria, another widely distributed species, has variable spores *(Figs. 5* and *6)* which are intermediate in size between the two described above. There is a tendency towards shorter, more clavate baculae. The trilete scar is more ornamented than that of *A. phyllitidis* but less so than that of *A. munchii*, having two rows of baculae.

Several members of subg. *Anemia* endemic to Brazil have specialized vegetative structures but conservative spore morphology. Four of these taxa were examined, but only one specimen of each was available for study due to scarcity. The first of these was *A. ouropretana*. This species differed from *A. phyllitidis* in its small spores *(Figs. 7, 8,* and *22)*, which were 40–50 μm in diameter. In addition, the baculae were distinctly rounded and slightly expanded towards the apex. This tendency was shared by spores of *A. radicans*, but this species is unique in that it relies upon vegetative as well as or instead of gametic reproduction. The sample examined *(Fig. 9)* possessed generally abortive or abnormally shaped and apparently non-functional spores as well as several elongated fronds bearing apical meristems. Since *A. radicans* is thought to be a sexually reproducing species (Lellinger, pers. comm.), the sample may have been atypical.

The spores of *A. pohliana (Figs. 10* and *21)*, a species also endemic to Brazil, resembled those of the other members already described, but nearly all of the spores examined in the single specimen available were either abnormally large or else were small and abortive. The scarcity of specimens, the discontinuity of the populations, and the intermediate nature of the fronds between those of several other members of the subgenus in addition to the abnormal spores may suggest that this species or this particular specimen is of hybrid origin. However, this requires further study.

The fourth Brazilian endemic examined, *A. rotundifolia (Figs. 11, 12,* and *23)*, had well formed, distinctly spherical spores. These were small for the subgenus,

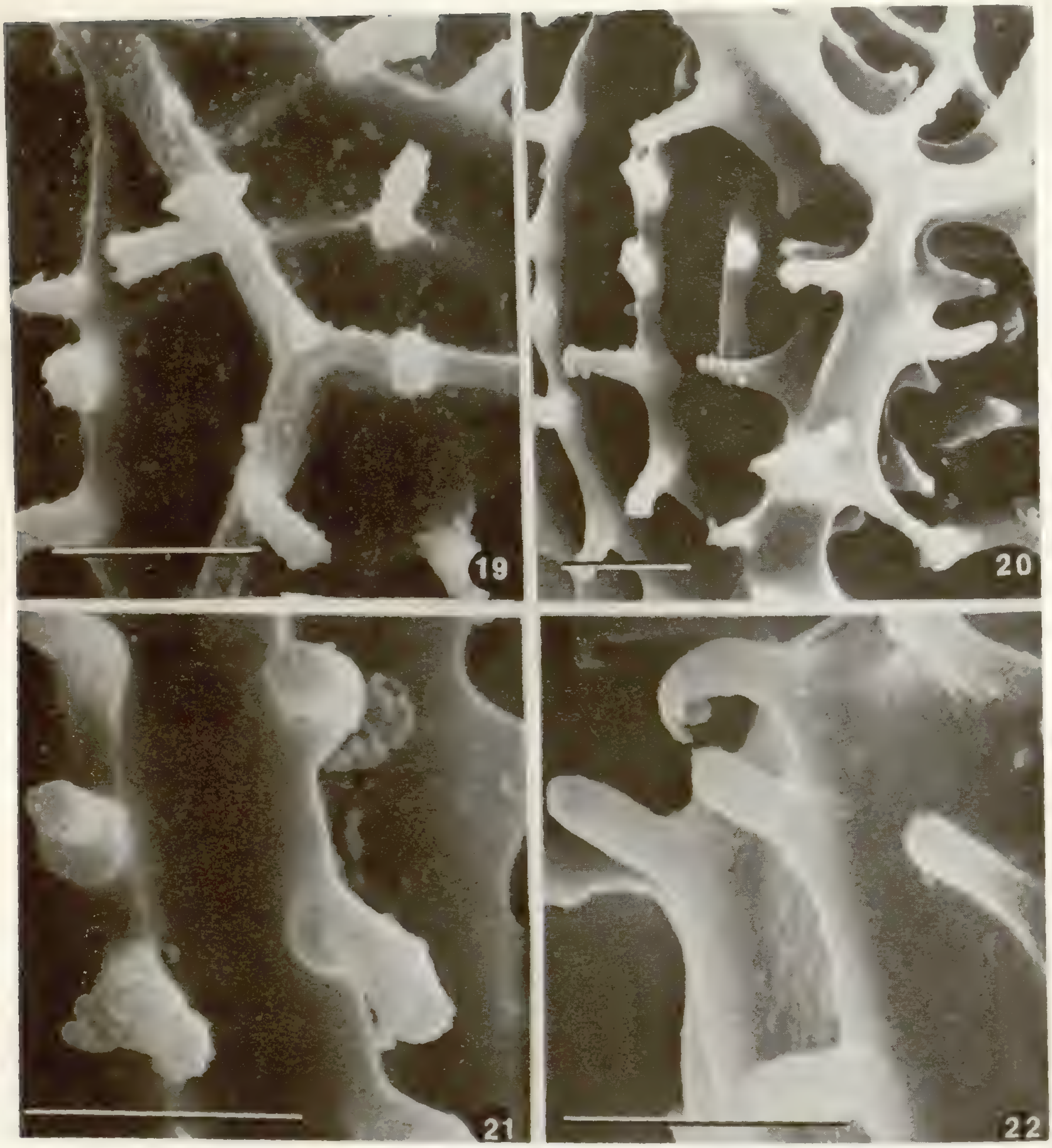
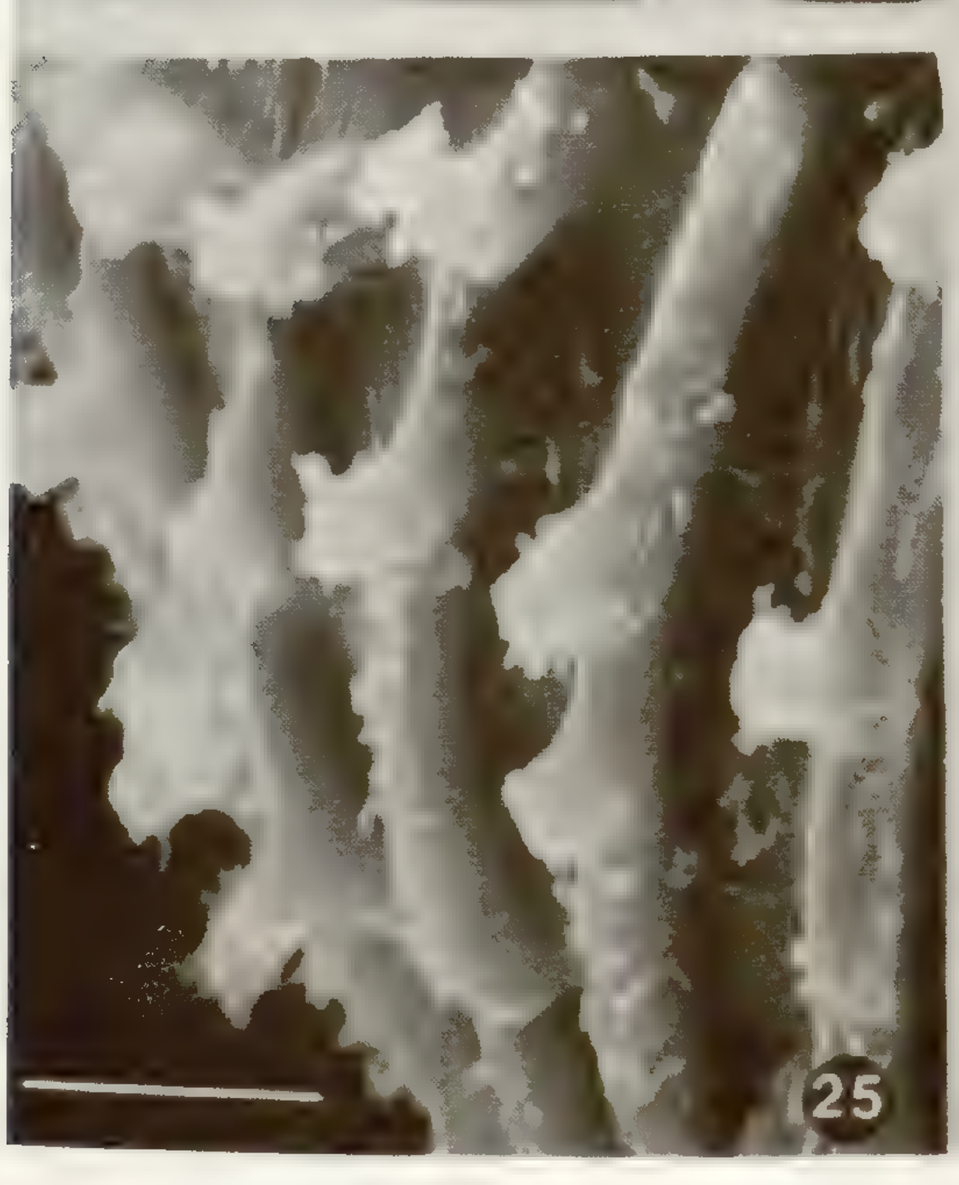


FIG. 19. *Anemia* spore ornamentation. *A. phyllitidis. Laughlin 2563.* FIG. 20. *A. munchii, Hill s.n.* FIG. 21. *A. pohliana. Chase s.n.* FIG. 22. *A. ouropretana. Irwin et al. 27976.* Line scale = 10 μm.

measuring 40 μm in diameter. The ridges lack microspines, and the baculae approach a clavate shape as in *A. ouropretana* and *A. radicans.*

The last group examined included two taxa, *A. oblongifolia* and *A. hirsuta*, both wide-ranging species. The spores of *A. oblongifolia* were seen to fall into two groups which were correlated with two vegetatively distinct groups of specimens. Group I may be exclusively Brazilian and can be characterized by semi-erect fertile fronds which are long-stalked (stipes up to 10 cm long) and which bear narrow pinnae 3–5 mm wide. The spores of this group *(Figs. 13, 14,* and *24)* differ from all of the other spore samples examined by the presence of wide ridges, narrow fossulae, and the complete absence of conspicuous baculae. In addition,



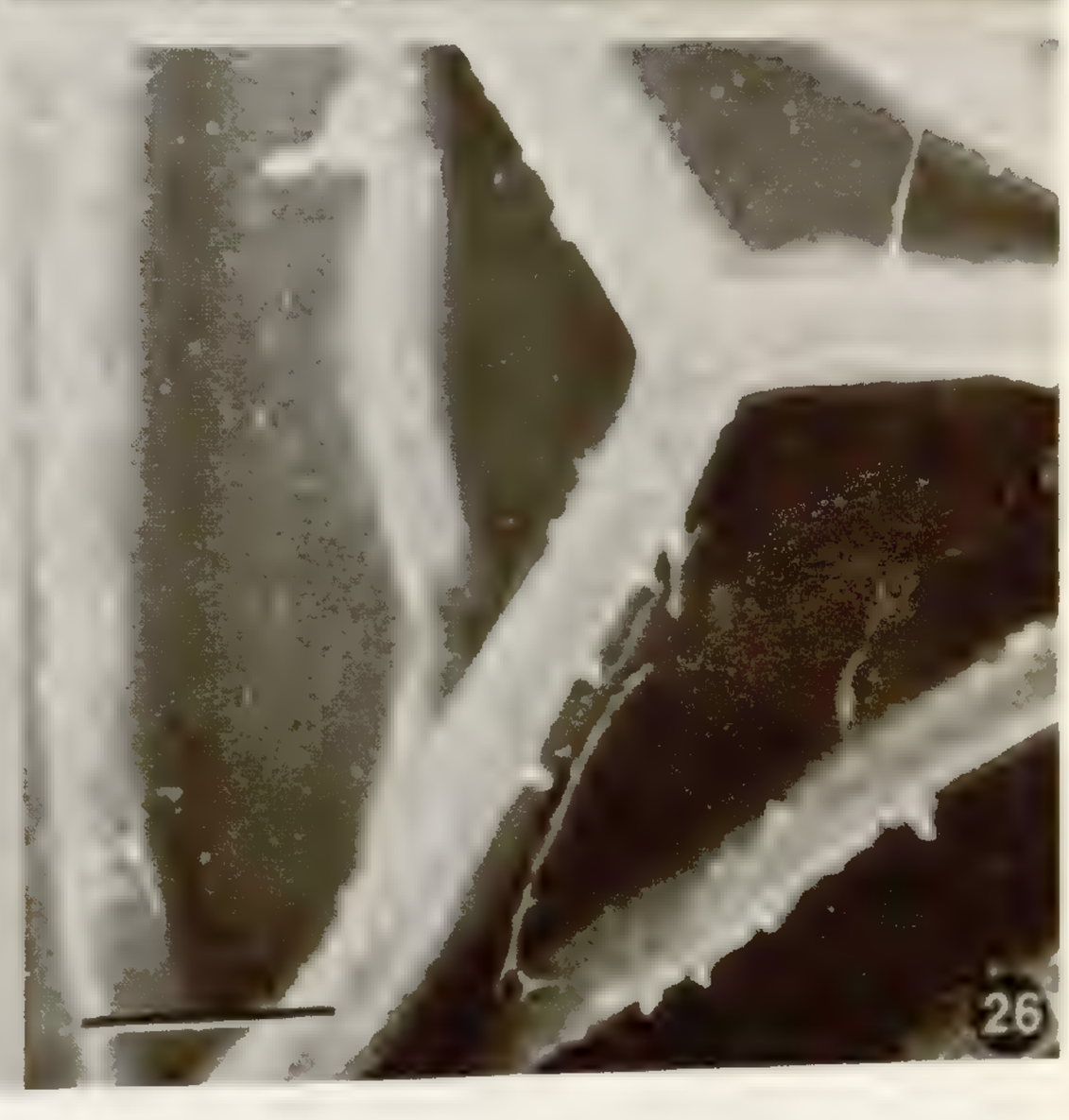


FIG. 23. *Anemia* spore ornamentation. *A. rotundifolia. Rose & Russell 20099.* FIG. 24. *A. oblongifolia,* Group I. *Irwin et al. 11793.* FIG. 25. *A. oblongifolia,* Group II. *Irwin et al. 13216a.* FIG. 26. *A. hirsuta. Hill 1643.* Line scale = 10 μm.

the spore angles are somewhat prolonged as seen in proximal view and the ornamentation of the ridges consists of small (2 μm), branched microspines. These characteristics are also typical of spores of members of subg. *Coptophyllum* (Hill, 1977). Plants in morphological Group II have low, short-stalked fronds (stipes up to 2–3 cm long) with comparatively broader pinnae 6–8 mm wide. The spores *(Figs. 15, 16* and *25)* have baculae typical of *A. phyllitidis* and its allies present in reduced form (3–5 μm long), and the occasionally branched microspines of the *Coptophyllum* group are also found among them. The fossulae and ridges are intermediate in width between typical examples of each subgenus. The spores

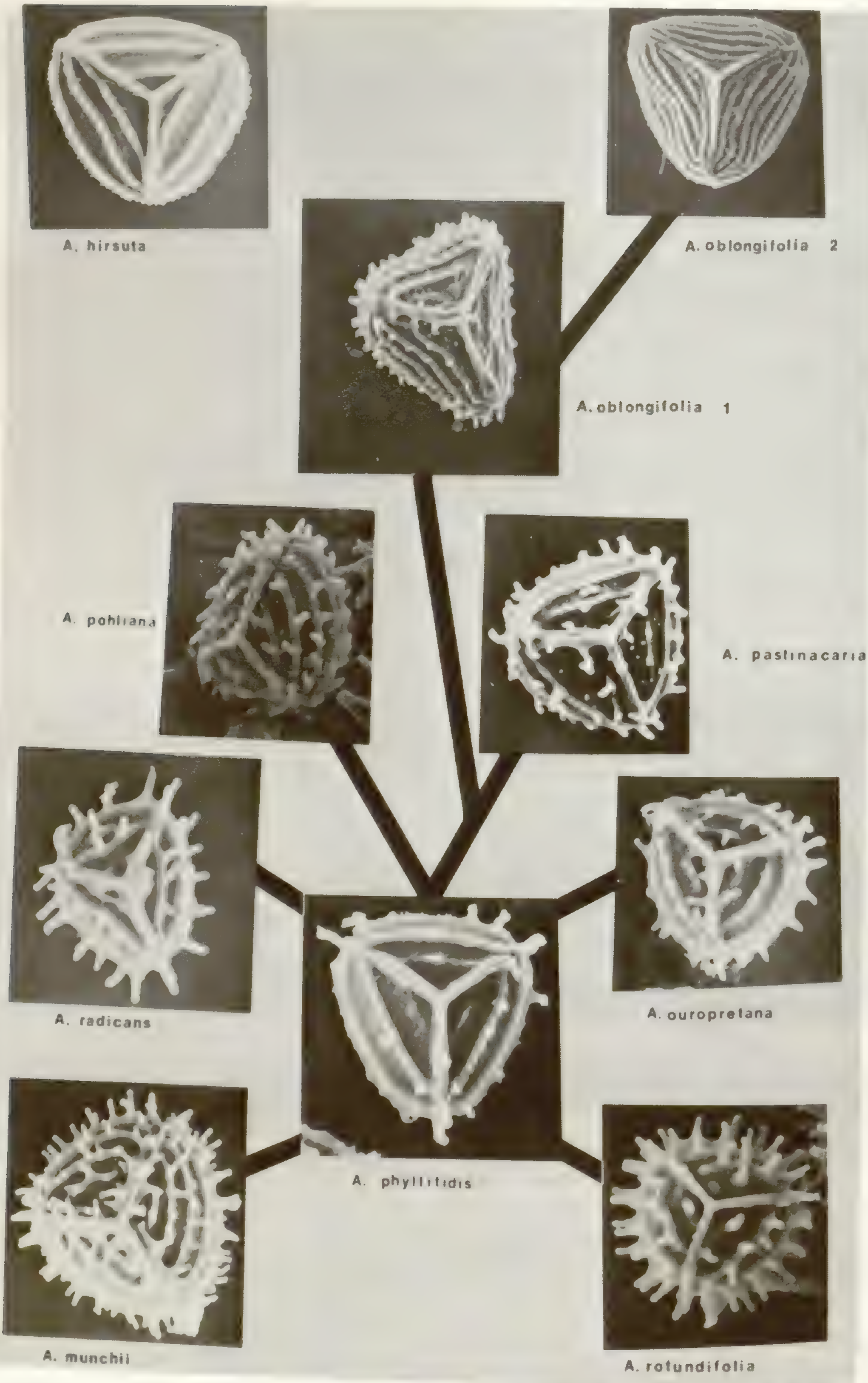


FIG. 27. Possible morphological relationships among selected spore types of subg. *Anemia*. Hypothetical connection with subg. *Coptophyllum* at upper right.

seem to provide a morphological link between the *A. phyllitidis* spore type and the Group I *A. oblongifolium* spore type described above, which is more typical of spores of subg. *Coptophyllum*.

The spores of *A. hirsuta (Figs. 17, 18,* and *26)* pose an interesting problem in subg. *Anemia*. The shape of the spores, the widely spaced, narrow ridges, and the unbranched microspines ornamenting those ridges are typical of those of *A. phyllitidis*, but the large baculae of that group are entirely absent, and the spore angles are slightly prominent.

DISCUSSION

Figure 27 illustrates a tentative scheme of morphologically related spore types to summarize the observations presented above. This scheme is not intended to represent a phylogeny, but is intended to express morphological similarities in the specimens examined. Basic to this arrangement are the variable spores of *Anemia phyllitidis*, to which several other spore types are connected. *Anemia radicans*, *A. ouropretana*, *A. munchii*, and *A. rotundifolia*, which are all restricted, specialized species, have spore types apparently related to and possibly even derived from the pool of variation seen in *A. phyllitidis*. *Anemia pohliana* may be a hybrid derived from members of this complex, but at any rate its spore type seems closely allied to that of *A. pastinacaria*, whose spores suggest a trend either towards baculae reduction as seen in spores such as those of *A. oblongifolia*, or in the opposite direction towards baculae elaboration as seen in *A. phyllitidis*. The *A. hirsuta* spore may be derived from that of *A. phyllitidis* directly through loss of the large baculae while retaining the microspines, or may be separately derived from that of *A. oblongifolia* by modification of the number of ridges and by simplification of the complexity of the microspines.

The problem requiring the most study is the morphological assessment of the *A. oblongifolia* complex. The spore analysis presented here suggests that more than one species actually is involved. In addition, the great resemblance of the spores of form 2 in *Fig. 27* (referred to as Group I in the text above) with those of subg. *Coptophyllum* may provide a link between the two subgenera. Since subg. *Coptophyllum* is considered to be the most primitive of the three subgenera (Mickel, 1962), this taxon may aid in our knowledge of the origin of subg. *Anemia*.

I would like to thank Dr. Elenor Cox and the Electron Microscopy Center at Texas A&M University for aid in obtaining access to the scanning electron microscope, Dr. John T. Mickel of the New York Botanical Garden for support while collecting spore samples in Oaxaca, Mexico, and Dr. David B. Lellinger of the U.S. National Herbarium for kindly lending specimens used in this study.

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The Development of Plantlets from Strobilus Branches in Lycopodium phlegmaria

Y. C. WEE*

Lycopodium phlegmaria L. is an epiphyte commonly found growing on the trunks and branches of forest trees in Singapore. It is a widely distributed species in the Old World tropics, ranging from Africa to Polynesia. Its pendulous stems are covered with spirally arranged, stiff, ovate-lanceolate leaves (*Fig. 1*). Both the sterile portions of the stems and the strobili branch dichotomously (*Figs. 1* and *2*). The sporophylls are smaller than the foliage leaves and are arranged more compactly along the branches. In most cases, the sporophylls are grouped terminally on determinate stems. However, instances of foliage leaves appearing along the strobilus branches have been observed (*Fig. 2*). This is reminiscent of the condition seen in *L. selago* L., where the fertile zones alternate with the sterile and the foliage leaves are not much different from the sporophylls (Bower, 1935, p. 200).

Recently, a portion of *L. phlegmaria* detached from the parent plant was found lying on damp ground on the secondary forest at the MacRitchie Catchment area in Singapore. It was still green, and the ends of the fertile branches showed growth following detachment. Under the humid conditions of the forest floor, the ends of the branches had reverted to vegetative growth and had produced one or two young plants each (*Fig. 4*). Roots had grown from the base of some of these young plants. In one instance, the extension of a strobilus branch was an elongate stem with long internodes (*Fig. 3*). At the nodes were leafy structures similar to the sporophylls. In the axils of these structures were obviously vegetative buds, some of which had developed into vegetative shoots (*Fig. 3*).

Longitudinal sections of the strobilus branches revealed the gradual transformation of the sporangia from fertile to sterile in the acropetal direction. The fertile, spore-containing sporangia had thickened outer cells along the inner and radial walls. Sterile sporangia lacked these characteristically thickened outer cells. Sporangia along the vegetative outgrowths were mere protuberances, without any differentiation whatsoever. As in ferns, root development was endogenous and very close to the vascular strand.

Placing the ends of strobilus branches from cultivated *L. phlegmaria* on moist vermiculite similarly stimulated development of vegetative shoots after about four months. The new growths had excessively elongate internodes, the sporophylls were smaller until foliage leaves were produced when the axis turned upwards. Roots formed at the points of turning after a further period of two to four months. These shoots could then be removed as plantlets.

These observations give support to Bower's (1908, p. 164) theory that foliage leaves essentially are sporophylls with the sporangia completely suppressed. In this respect, it should be noted that the strobili of *L. obscurum* L. and *L. flabel-*

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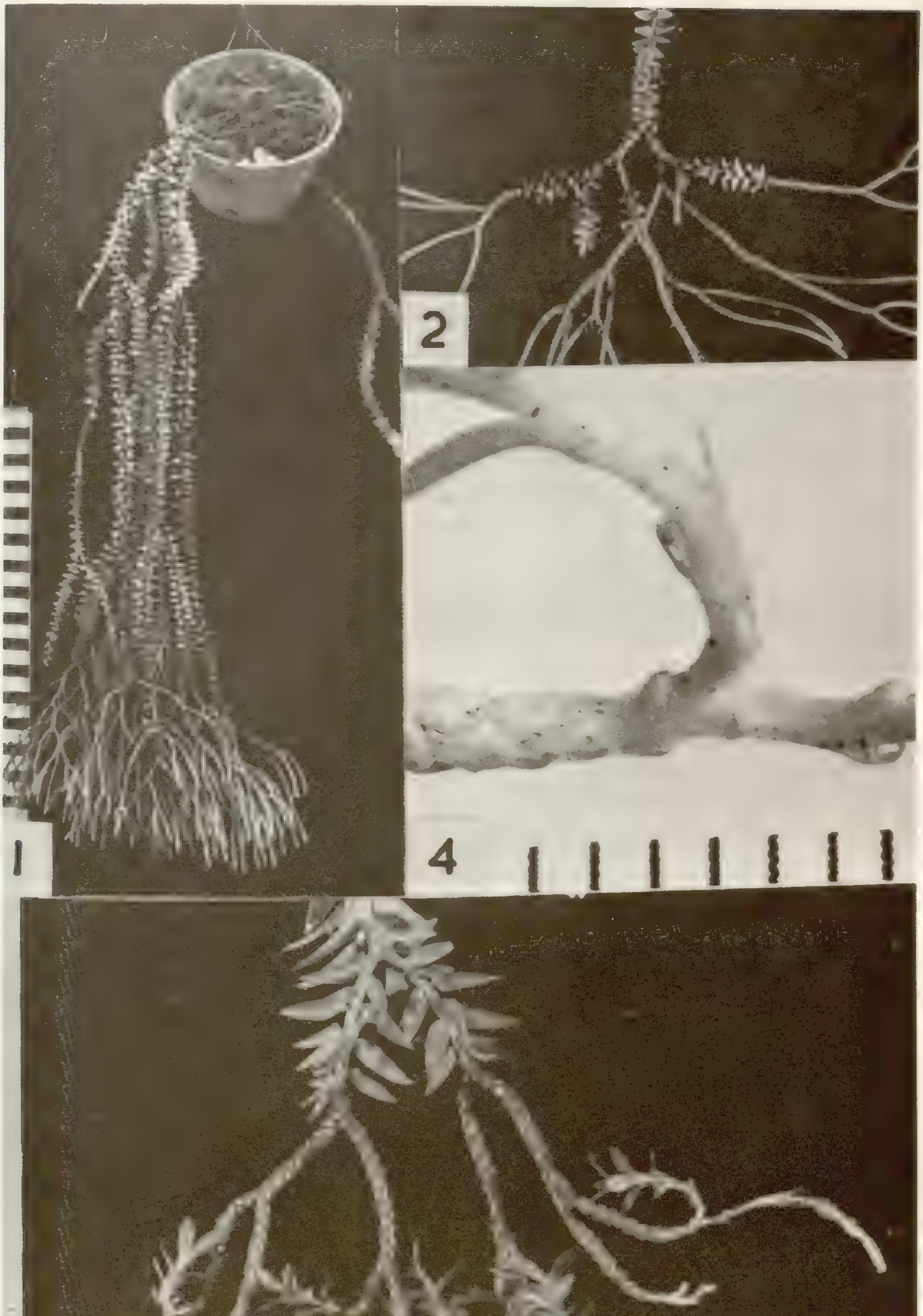

FIGS. 1–4. *Lycopodium phlegmaria*. FIG. 1. Potted plant showing the pendulous habit and dichotomously branched strobili (scale in cm). FIG. 2. Strobilus branches showing groups of foliage leaves. FIG. 3. Detached portion of plant found on the forest floor showing branch tips developing into plantlets (scale in mm). FIG. 4. Close-up of portion of *Fig. 3* showing new growth at the end of a strobilus branch (scale in mm).

liforme (Fern.) Blanch. also have been observed to produce vegetative extensions, but not plantlets (Bierhorst, 1971, p. 15). In *Selaginella*, however, Goebel (1930, p. 657) managed to induce pieces of strobili to develop foliage leaves by placing them on a moist medium.

I wish to record my thanks to Prof. A. N. Rao for his assistance in the anatomical study and for critically reviewing this paper; to Mr. J. Wee for bringing the piece of *L. phlegmaria* to my attention and for technical assistance; and to Mr. D. Teow for the photographs.

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Incidence of Epiphytism in the Lycopsids

JOSEPH M. BEITEL*

Epiphytism in pteridophytes is well known, with the families Hymenophyllaceae, Polypodiaceae, and Aspleniaceae each containing a large number of epiphytic species (Copeland, 1947). In a recent article on epiphytism (Madison, 1977), the systematic composition and major features of vascular epiphytes were examined, based on observations of living plants and a survey of specimens in the Gray Herbarium of Harvard University. Sixty-five families of vascular plants were listed, including the Psilotaceae, Ophioglossaceae, Schizaeaceae, Hymenophyllaceae, Polypodiaceae, Aspleniaceae, Aspidiaceae, and Davalliaceae. However, two major pteridophyte families, the Lycopodiaceae and the Selaginellaceae, were not included. These omissions in Madison's enumeration seriously distort the true incidence of pteridophytic epiphytes.

A survey of the herbaria at the University of Michigan, the New York Botanical Garden, the Missouri Botanical Garden, the Field Museum, and the Smithsonian Institution revealed a very substantial number of epiphytic species in *Lycopodium s.l.* In fact, of the 374 species of *Lycopodium s.l.* examined, 192 species (51%) were epiphytic. All of the epiphytic species are in the segregate genus *Huperzia s.l.* (commonly treated as *Lycopodium* subg. *Urostachys*). *Huperzia*, including its 93 terrestrial members, accounted for 76% of all the species of *Lycopodium s.l.* examined. *Huperzia* species are far more common and diverse in the tropics than in the temperate zone. Only a few species occur in North America north of Mexico, of which the best known are the two terrestrial species *L. selago* and *L. lucidulum*, the epipetric species *L. porophilum*, and the epiphytic species *L. dichotomum*.

The epiphytic members of *Huperzia* fall into two classes, with intermediates between the classes grading from one extreme to the other. At one extreme there is little or no differentiation of the sporophylls, the sporangia being borne on photosynthetic leaves on normal shoots. At the other extreme, there is strong differentiation of the sporophylls, which are also aggregated into dangling tassels. With few exceptions, the branch systems are pendent, the base of the plant being attached by a mass of roots to boughs and crotches of the supporting trees. Gametophytes of epiphytic species are found buried in leaf mold and mosses in the same habitat as the sporophytes (Bierhorst, 1971, p. 22).

The large number of epiphytic *Huperzia* (192 species), when compared with Madison's enumeration, ranks this group as the 13th largest family of vascular epiphytes (out of a total of 65 families) and the 12th largest genus of vascular epiphytes (exclusive of the genera of the Orchidaceae, which was not broken beyond the family level in Madison's list).

A comprehensive survey of the spike-mosses (*Selaginella*) would probably result in the discovery of some epiphytes, although the great majority of species are terrestrial or epipetric. At least five epiphytes are known in *Selaginella*.

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Selaginella oregana D. C. Eaton is an isophyllous spike-moss of the Pacific Northwest rainforest, where it typically hangs from deciduous trees such as *Acer macrophyllum* (Hitchcock et al., 1969, p. 32), and *S. zahnii* Hieron. is a heterophyllous spike-moss from New Guinea and the Admiralty Islands, where it grows among mosses and filmy ferns on trees (Wagner & Grether, 1948, p. 65). Three species of *Selaginella* are known to be facultative epiphytes, although they more commonly are epipetric: *S. involvens* (Swartz) Spring from China, Japan, Taiwan, and the Ryukyu Islands (Walker, 1976, p. 38), *S. molliceps* Spring from Africa and Madagascar (Tardieu-Blot, 1964, p. 25), and *S. versicolor* Spring from West Africa (Alston, 1959, p. 16).

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REVIEW

"THE PTERIDOPHYTES OF KANSAS, NEBRASKA, SOUTH DAKOTA AND NORTH DAKOTA, U.S.A.," by Aleta Jo Petrik-Ott, Nova Hedwigia Beiheft 61:1–332. 1979. Dm. 100 (ca. $50.00).—Of all the United States regional fern Floras, this is probably the most complete in its treatment. Sixty-five pteridophyte taxa are included. Each is dealt with at length by means of a synonymy, a description including chromosome data when known, the time of sporulation, the habitat, United States and northern Great Plains distribution maps, specimen citations, notes, and common names. The author's own illustrations add greatly to the book. The keys are accurate and useful. The bibliography includes about 200 items. An annotated list of excluded names and the like will help lay to rest taxa erroneously included in the flora in the past. A glossary, indices to Latin and common names, and an addendum conclude the volume. This work surely is indispensible for critical taxonomic and floristic work in the upper great plains.—*D.B.L.*

Cyrtomium fortunei in Louisiana and Mississippi

GARRIE P. LANDRY,* MICHAEL ISRAEL,**
ROBERT SCHWARZWALDER, JR.,* and R. DALE THOMAS***

On September 2, 1978, we observed a few plants of *Cyrtomium fortunei* J. Smith in the labyrinth of ravines of the Tunica Hills region 2 miles northwest of Weyanoke, in West Feliciana Parish, Louisiana (*Israel* in 1979, LSU). A second population of approximately 80 plants was discovered on September 10, about three miles from the first location in deep ravines on Ouida Irondale Road 4 miles east from La-66 (Landry 78574, LSU, MICH). During the exploration of ravines on September 17 in Wilkinson County, Mississippi, which is due north of West Feliciana Parish, a single plant of *C. fortunei* was observed growing at a waterfall on Clark Creek, north of the settlement of Pond (*Landry 78593*, LSU). Following these discoveries, we found that *C. fortunei* had been collected by Dr. R. Dale Thomas, 3 miles North of Tunica, Louisiana in October, 1974 (*Thomas 42096*, NLU, LSU). The collection was identified by Dr. A. Murray Evans. The discovery of this fern represents a new addition to the presently known floras of Louisiana (Thieret, 1972) and Mississippi (Evans, 1978).

Cyrtomium fortunei is characterized by a short, erect rhizome covered with dark, lanceolate to ovate, acuminate scales. The fronds are pinnate with 23 or more pairs of lanceolate, dull green pinnae having a prominent, darkened midvein. *Cyrtomium fortunei* is easily recognized by its papyraceous fronds and minutely serrate pinnae, as opposed to the commonly cultivated *C. falcatum* Presl, which has coriaceous fronds with entire, glossy pinnae.

Nearly all stages of reproduction were observed in the populations of *C. fortunei*. The largest plants were 75–90 cm high and had all fertile fronds. But plants 30 cm or less high also had some fertile fronds. Profuse reproduction was evident from the large number of sporelings having two or three fronds. The largest plants were predominantly on the upper sides of the ravines, whereas the smallest were confined to the ravine bottoms.

The Tunica Hills region is characterized by hills with loess deposits ranging from 1 to 60 m thick. Elevations in the area vary from 60 to more than 90 m above sea level. The hills are highly eroded by streams, and form narrow ridge tops with correspondingly steep to vertical slopes ending in ravines. The vegetation is classified as a mixed mesophytic forest association modified by *Magnolia* and other subtropical broadleaf species. In all locations, the associated species were *Magnolia grandiflora*, *Fagus grandifolia*, *Ilex opaca*, *Cornus florida*, and *Arundinaria gigantea*. Other pteridophytes observed include *Adiantum pedatum*, *Cystopteris fragilis*, *Athyrium pycnocarpon*, *A. thelypteroides*, *Polystichum acrostichoides*, and *Equisetum hyemale*.

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Cyrtomium fortunei was introduced into cultivation as early as 1866 (Christensen, 1930). Although once popular horticulturally, it has been superseded by more attractive species such as *C. falcatum*. *Cyrtomium fortunei* in the Tunica Hills region may have originated as an escape from the numerous, old plantation gardens of the area. Naturalization of cultivated pteridophytes in Louisiana is not without precedent; *Selaginella braunii* Baker and *S. uncinata* Spring both have become established (Landry, unpubl.). Although MacDougal (1976) found *C. fortunei* on brick walls in Charleston, South Carolina, in our opinion these plants qualify as escapes or as adventives, but are scarcely naturalized. The occurrence of *C. fortunei* in this region may represent the first report of its naturalization in the United States (W. H. Wagner, Jr., pers. comm). We would like to express our sincere appreciation to Dr. Warren H. Wagner, Jr. for his assistance in preparing this article.

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The Fine Structure of the Pre-meiotic Stages of Sporogenesis in Onoclea sensibilis

NORMAN P. MARENGO*

Ultrastructural features of the dividing meiocyte of *Onoclea sensibilis* L. were described by the author (1977), and those of the young spores arising from this cell by Marengo and Badalamente (1978). Since a light microscopic study of this species by the author (1949) showed an apparent decrease in size of cytoplasmic inclusions from the sporangium initial to the spore mother cell, it is of interest to elucidate these changes on the ultrastructural level.

Individual sporangia dissected from young fertile fronds were routinely fixed in glutaraldehyde followed by osmium tetroxide and embedded in Epon (Spurr, 1969). Sections 0.5μm thick were cut from individual sporangia and were examined by phase contrast microscopy without staining. From sporangia identified as containing pre-meiotic stages in sporogenesis, thin sections were cut with a diamond knife, stained with uranyl acetate and lead citrate, and examined with an Hitachi HU-11A electron microscope.

The sporangial initials (*Fig. 1*) appear to contain large, osmiophilic bodies (*Fig. 1*, t) which resemble closely the tannin accumulations described by Ledbetter and Porter (1970). The appearance of vacuoles (v) within these bodies is followed by their disappearance in the later stages of sporogenesis, including newly formed spores. Mitochondria (m) appear hardly larger than those in later stages and in newly formed spores. Their internal structure, however, differs from that of mitochondria in newly formed spores. Cristae appear not to be shelf-like, but rather mitochondrial material separated by internal cavities. This peculiar and distinctive internal structure persists through at least the early prophase of meiosis (*Fig. 6*, m), following which their cristae extend as plates, continuous across the mitochondrion (Marengo, 1977).

The osmiophilic bodies are still present in early sporogenous cells (*Fig. 2*, t), with an occasional vacuole apparently replacing the tannin mass (*Fig. 2*, v). By the time the sporogenous cells approach the rounded-up meiocyte stage, the osmiophilic bodies have disappeared and lipid droplets appear in the cytoplasm (*Fig. 3*, L).

In the dividing sporogenous cell in anaphase (*Fig. 4*), the mitochondria appear concentrated in the polar regions of the spindle. The distribution of mitochondria at mitotic anaphase appears to contrast markedly with that of the meiotic anaphase I, where the mitochondria are concentrated at the edge of the spindle preparatory to invading it, and form the mitochondrial plate characteristic of interphase following the first division as well as all phases of the second meiotic division (Marengo, 1949, 1977).

In the early prophase of the first meiotic division (*Fig. 5*), spore mother cell polarity is reflected in a concentration of mitochondria at the base of a barely

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FIG. 1. Part of a sporangial initial showing dense accumulations of tannin (t), an incipient vacuole (v), an amyloplast (a), and several mitochondria (m). Base of the initial is at the left. × 11,516. FIG. 2. Part of a sporogenous cell showing persistent tannin bodies (t), mitochondria (m), and an amyloplast (a). × 11,167.

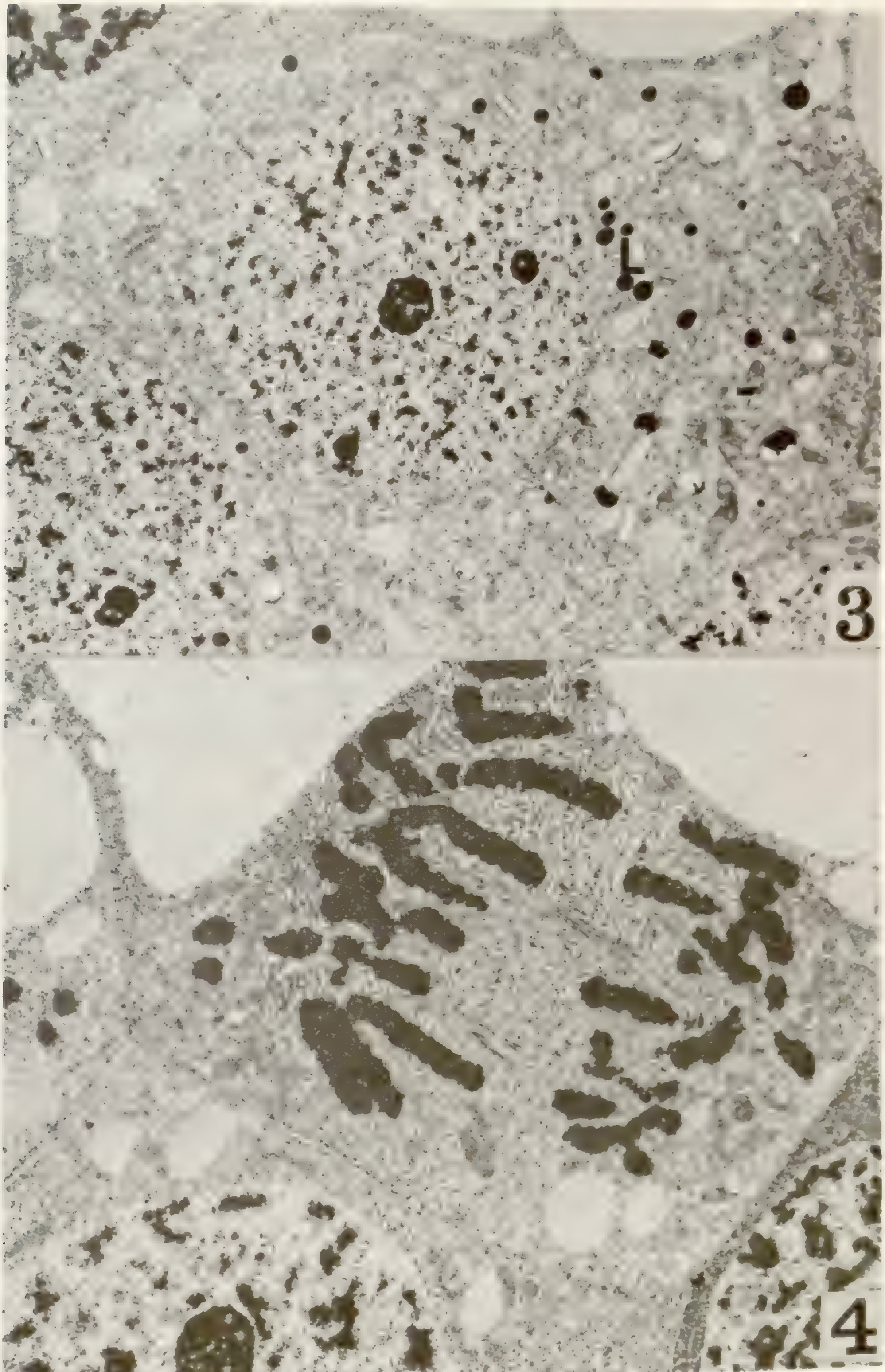

FIG. 3. An older sporogenous cell just prior to "rounding-up" into the spore mother cell. Dense tannin bodies are absent and lipid droplets (L) occur. × 4,480. FIG. 4. Sporogenous anaphase showing mitochondria concentrated in polar regions of the spindle, × 7,484.

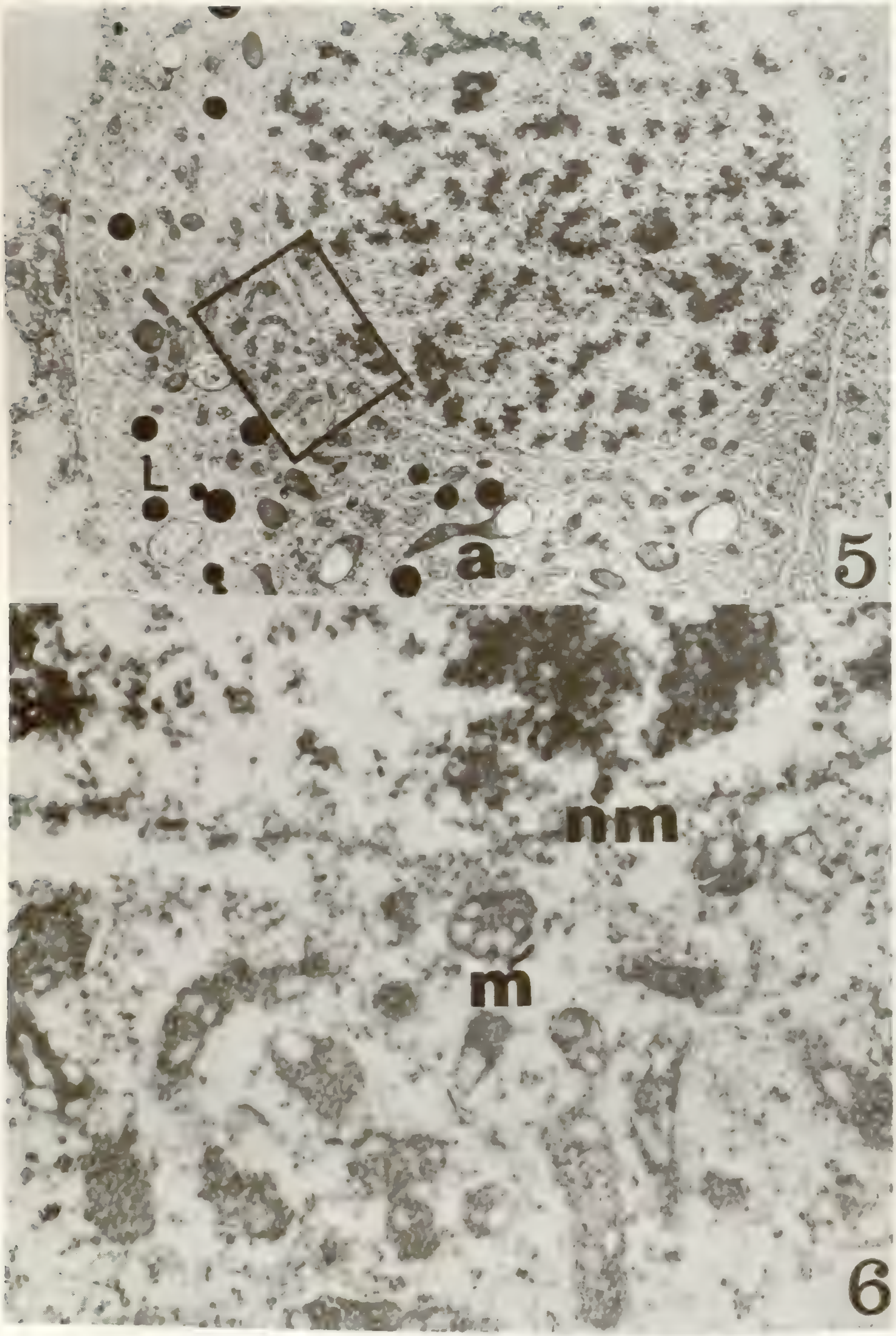

FIG. 5. Early prophase of the first meiotic division. The polarized chromosomes have a mitochondrial concentration at their base (barely discernible in the marked area), × 12,272. FIG. 6. Enlargement of marked area of *Fig*. 5, showing mitochondria (m) with atypical internal structure and nuclear membrane (nm) undergoing the disorganization characterizing the onset of meiosis, × 33,750.

discernible (by electron microscopy) polarized "bouquet" of chromosomes (Marengo, 1949). This pachytene "bouquet" of the meiotic prophase has been described in animal meiosis *(Cicada)* by Shaffer (1920) and by Plough (1917) in *Rhomaleum*.

An enlargement *(Fig. 6)* of the marked area in *Fig. 5* shows mitochondria with still peculiar and distinctive internal structure and a disorganized nuclear membrane (nm) reflecting the onset of meiosis.

It appears from the sequence of events described that the large, "plastid-like" inclusions of the author's paper of 1949 were in all probability the osmiophilic accumulations of tannin described herein, since the mitochondria, although undergoing an internal reorganization during the pre-meiotic stages of sporogenesis, show no appreciable decrease in size.

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REVIEW

"ATLAS OF FERNS OF THE BRITISH ISLES," edited by A. C. Jermy, et al. 101 pp. Botanical Society of the British Isles and the British Pteridological Society, London, 1978. ISBN 0-901158-01-1. £ 3.50.—This atlas updates Perring and Walters' "Atlas of the British Flora" (1962). The nomenclature follows "Flora Europaea," with a few recent and necessary changes. The 95 maps center one dot for each 10 km square, and will be of interest mostly to students of the British flora. Accompanying each map, however, is a brief paragraph containing phytogeographical and ecological notes of great value to taxonomists and horticulturalists. Usually a reference to a specific, detailed paper concerning the taxon also is given. The notes on differentiating difficult species and hybrids also are very welcome. Problems of ecology and taxonomy still awaiting resolution are pointed out. This volume is more than an atlas, and is a welcome addition to the pteridophyte literature for Britain.—*D. B. L.*

Apical Dominance in Anemia phyllitidis Gametophytes

THOMAS L. REYNOLDS*

The phenomenon of apical dominance (generally defined as the inhibition of lateral buds or meristems by the apical bud or meristem) occurs generally throughout the plant kingdom and does not appear to be limited to higher vascular plants. Albaum (1938a) demonstrated that the central growth zone, located in the indentation of the roughly heart-shaped prothallus of *Pteris longifolia,* was analogous to an apical meristem. If this apical meristem was excised from the prothallus, numerous adventitious gametophytes, each with a central growth zone, would arise from the previously inhibited cells. The meristematic zone was considered responsible for the maintenance of apical dominance as long as there was a continuum of living cells between this meristem and the rest of the prothallus. As far as I am aware, the present report is the first to document meristem-induced apical dominance in isolated prothallial tissues where there was a total lack of cellular continuity between the meristem and the affected cells.

MATERIALS AND METHODS

Ripe sporangia of *Anemia phyllitidis* (L.) Swartz were collected from greenhouse-grown plants. Prior to the experimental manipulations, the spores were surface sterilized by suspending them for 1 minute in a freshly made solution of 1% sodium hypochlorite (Clorox), followed by several rinses in sterile, distilled water. The final spore suspension (10 ml) was transferred to a sterile culture tube. Subsequent dilutions of this suspension were made until a spore density of 8.0×10^2 spores/ml was obtained. One milliliter aliquots of this suspension were aseptically transferred to 125 ml Erlenmeyer flasks containing 67 ml of Miller and Miller's (1961) sterile, modified Knop's medium. The spore cultures were placed on a shaker under 400 ft-c of white light for 6 to 8 weeks at 25 ± 2°C. The gametophytes which formed served as stock material for the experiments.

Nearly mature, cordate gametophytes were harvested in a sterile transfer room. They were graded for uniformity in size and were cut into equal halves. Ten apical halves each possessing a meristematic notch and ten basal halves each lacking a meristematic notch were placed in a single Petri plate containing filter paper moistened with 10 ml of the sterile medium. These cultures were sealed with Parafilm and returned to 400 ft-c white light for 21 days. During this period, the halved gametophytes were provided fresh medium weekly. Basal halves cultured independently of the apical halves served as a control. Counts of the number of adventitious gametophytes formed were made at the end of three weeks. Each experiment was performed in duplicate, and the entire series of experiments was repeated once.

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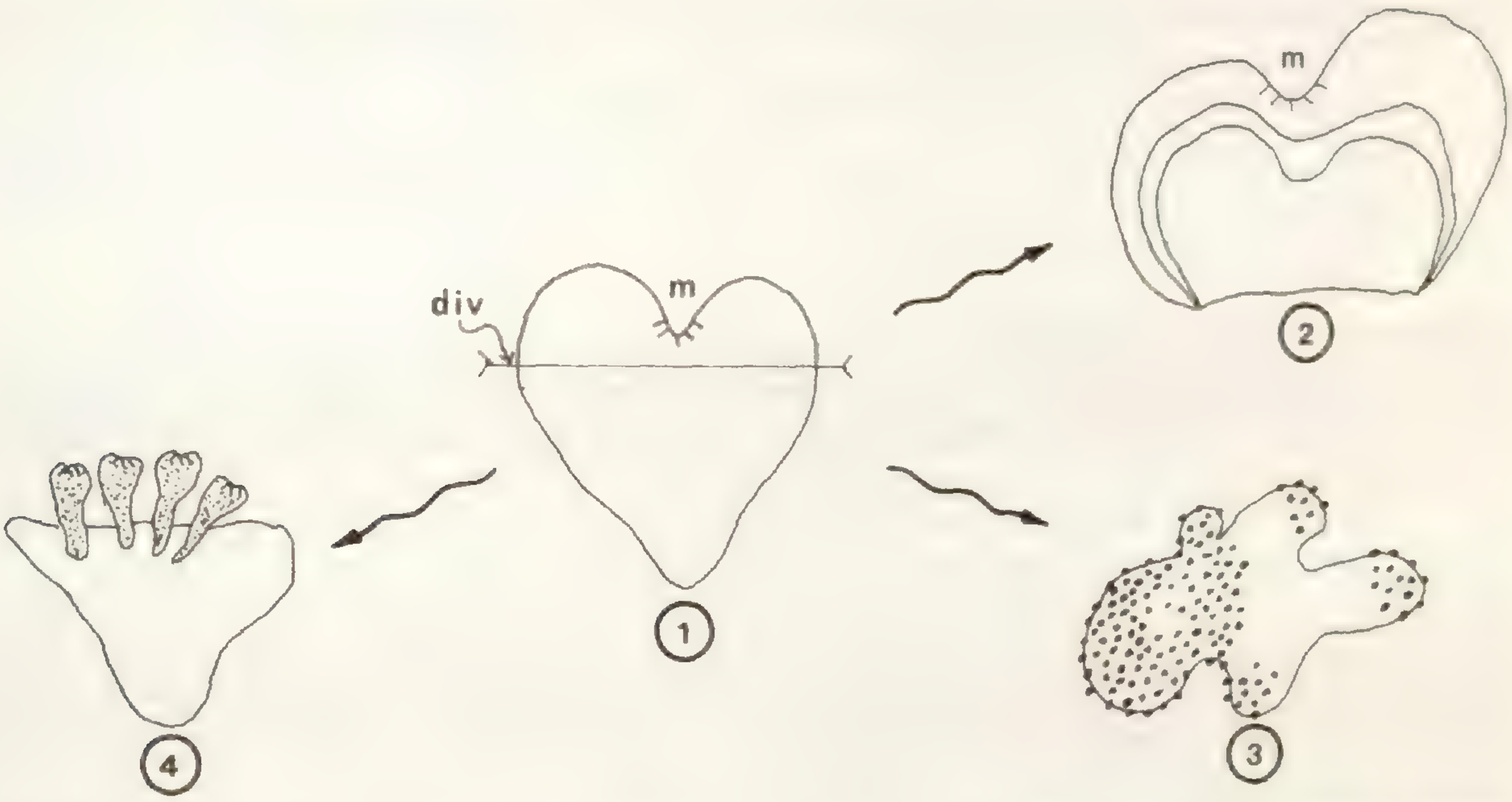
OBSERVATIONS AND DISCUSSION

When excised apical and basal halves were cultured together (*Figs. 1–3*), the formation of heart-shaped, bisexual gametophytes by the basal halves was almost completely suppressed; only one out of 200 explants produced a notched gametophyte in 21 days. The apical halves continued their normal differential growth to form cordate prothallia with both antheridia and archegonia (*Fig. 2*). Each basal half produced numerous antheridia but no archegonia, became spatulate in form, and completely lacked a central meristematic zone (*Fig. 3*). These plants retained their distinct morphology as long as they remained in culture with the meristematic plants. When basal fragments were cultured alone (for 14 days as a control) or were removed for 14 days from the influence of the apical explants, there was a rapid proliferation of lobes with notched meristems and archegonia in 200 out of 200 explants (*Fig. 4*).



FIGS. 1–4. Apical dominance in the gametophyte of *Anemia phyllitidis*. FIG. 1. Division of a nearly mature, cordate gametophyte into apical and basal portions. FIG. 2. Continued normal development of an apical half over a 3-week period. Eventually a single, whole gametophyte forms. FIG. 3. Basal half cultured in association with apical halves forms an amorphic male gametophyte. The black dots represent antheridia. FIG. 4. Basal half cultured alone produces numerous, adventitious gametophytes (stippled outgrowths), each with a notched meristem. Abbreviations: div = division, m = apical meristem.

These results indicate that, contrary to the well documented reports on other plants (Miller, 1968), the apical meristem of *Anemia* can exert its influence over the mature basal cells of the gametophyte without tissue continuity between the two regions. This example of apical dominance is probably maintained through the production of some diffusible chemical substance by the meristem, since basal halves readily form adventitious gametophytes when removed from the influence of the apex. However, the regulatory mechanism does not require a junction of living tissue to be effective.

The exact nature of the controlling chemical produced by the apex is, as yet, unknown. Albaum (1938b) proposed that the meristem acts as a source of auxin which is transported basipetally in intact gametophytes to inhibit the division of mature cells. Voeller (1966) established that *Anemia* possesses an antheridogen system and, at least initially, produces two types of gametophytes. The male type is spatulate in outline, lacks a notch meristem, and bears only antheridia. The hermaphroditic type is cordate, possesses a notch meristem, and produces both antheridia and archegonia. In multispore culture, both morphological forms exist at the same time, but the male is induced only by the presence of an antheridogen produced by the meristem of the hermaphrodite. Due to the limits of information provided by this study, the possible role of antheridogen in suppressing or modifying the expression of totipotency by differentiated cells cannot be ascertained. It does seem plausible, however, that antheridogen and possibly other substances, such as auxin, produced by the apex may be intricately involved in apical dominance and the maintenance of the normal form of intact gametophytes.

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SHORTER NOTES

A NEW COMBINATION IN ASPLENOSORUS.—Recently, Taylor and Mohlenbrock (Amer. Fern J. 67:66. 1977) published the name *Asplenium* × *herb-wagneri* for the hybrid between *Asplenium pinnatifidum* and *A. trichomanes*. This is appropriate as long as the Walking Fern is considered as a species of *Asplenium*. However, when the Walking Fern is considered as the separate genus *Camptosorus*, as it commonly is, all taxa containing genomes of both *Asplenium* and the Walking Fern must be considered as part of the hybrid genus *Asplenosorus*. In the above-mentioned case, the hybrid between *Asplenium (Asplenosorus) pinnatifidum*—itself the fertile hybrid between *Camptosorus rhizophyllus* and *Asplenium montanum*—and *Asplenium trichomanes* has one set of chromosomes from each of *Camptosorus rhizophyllus*, *Asplenium montanum*, and *Asplenium trichomanes*. The name for this hybrid thus becomes *Asplenosorus* × **herb-wagneri** (Taylor & Mohlenbrock) Mickel.—*John T. Mickel, New York Botanical Garden, Bronx, NY 10458.*

CHEILANTHES ALABAMENSIS NEW TO KENTUCKY.—In the past, *Cheilanthes* has been represented in the flora of Kentucky by *C. lanosa* (Michx.) D. C. Eaton and *C. feei* Moore. Both are xerophytes restricted to various types of dry, rocky outcrops. *Cheilanthes lanosa* is widespread in the southern and western counties of Kentucky. on both calcareous and non-calcareous substrates; *C. feei* is known only from crevices in blocky Silurian dolomite cliffs in Bullit County, where it reaches the southeastern limit of its range. Now a third species of *Cheilanthes*, *C. alabamensis* (Buckl.) Kunze, can be added to the Kentucky flora. The Alabama Lip Fern is frequent on limestone cliffs and ledges from Tennessee, Missouri, and Kansas south to northern Florida, Louisiana, Texas, and Mexico. We suspected that it might occur in Kentucky due to its presence in Montgomery County, Tennessee on bluffs along the Red River.

On 15 April 1979, we searched for likely sites on the Dot topographic sheet covering south-central Logan County. We chose to examine cliffs along a sharp bend of the Red River where it loops into Kentucky. The high, limestone cliffs were predominantly sheer and very dry, not the typical habitat of *C. alabamensis*. After a short search, we found an outcrop of well weathered limestone with an abundance of small cavities and recesses. Soon we located a small clump of juvenile *C. alabamensis* plants. About a hundred yards further, we discovered a large specimen from which we made collections (*Cranfill 3761*, APSC, KY). Plants associated with the Lip Fern include *Aquilegia canadensis, Arabis laevigata, Heuchera pubescens,* and *Taenidia integerrima*, as well as the ferns *Asplenium platyneuron, A. resiliens, Cystopteris bulbifera, C. tennesseensis, Pellaea atropurpurea*, and *P. glabella*. In addition, there was an abundance of both epiphytic (on *Ulmus americana*) and epipetric *Polypodium polypodioides*.

No additional plants of *C. alabamensis* were discovered during an intensive, two-hour search. The apparent rarity of this fern probably stems from two related factors: the northern locality with its harsh winters and the abundance of *Heuchera* and *Polypodium* competing at the site. Winter die-back, which is not normal in *C. alabamensis*, was evident in both clumps, especially in the juveniles. The winter climate may weaken the gametophytes and young sporophytes sufficiently so that they can barely compete with the *Heuchera* and *Polypodium*. Although abundant on the cliff face, these plants are most robust in the niche that the fern finds most suitable. These factors could account in part for the frequency of all three plants. An intensive investigation of similar cliffs in Todd and Christian counties would very likely reveal additional stations for the Alabama Lip Fern.—*R. Cranfill, Division of Biological Sciences, University of Michigan, Ann Arbor, MI 48109* and *Laurina Lyle, Department of Botany, Austin Peay State University, Clarksville, TN 37040.*

SEXUALITY IN ASPLENIUM RESILIENS.—The widespread species *A. resiliens* Kunze ranges from eastern, central and southwestern United States to southern South America. In the southeastern United States, cytological investigation by Wagner (Amer. Fern J. 56:3–17. 1966) has shown it to be an apogamous triploid producing 32 spores per sporangium. This condition is strongly correlated with an apogamous life cycle, whereas the 64-spored condition indicates normal sexual reproduction.

In preparing a treatment of *Asplenium* of the Chihuahuan Desert region, I counted spores from the sporangia of 50 different collections of *A. resiliens* deposited at TEX/LL. These ranged from central Texas and southern Arizona to southern Mexico, with a few from South America, but most were from the Chihuahuan Desert region of Texas and Mexico. Several unopened sporangia per specimen, from separate individuals when possible, were counted. Almost all specimens yielded counts of ca. 32 spores per sporangium (rarely ca. 64 aborted spores). However, in two specimens from the Chisos Mountains of west Texas, ca. 64 spores per sporangium were counted in each of five sporangia from each sheet. The spores were smaller than in the other populations, but otherwise were normal.

Apparently this is the first report of sexuality in this species. The putative sexual plants are morphologically indistinguishable from the apogamous ones. Thus, both sexual and apogamous forms appear to occur in *Asplenium resiliens*, a situation similar to that described by Wagner, Farrar and Chen (Amer. Fern J. 55:171–178. 1965) for *Pellaea glabella* var. *glabella*.

The 64-spored specimens, both from Brewster County, Texas, are: Green Gulch, Chisos Mountains, 28 Mar 1937, *Warnock 608;* and South River [Rim], 26 Aug 1937, *Warnock 608*.

Although both bear the same collection number, the former bears the collector's signature on the label, and the latter label is typed and includes at least one clear error. It is likely that the latter label is in error and that both sheets represent a single collection from Green Gulch. Collections of *A. resiliens* from Green Gulch made during other years (*Correll 13666; Warnock & Tharp 6837; Wendt & Lott 2144, 2144A*) and numerous other Chisos Mountains specimens examined uniformly display 32 spores per sporangium.—*Tom Wendt, Rama de Botánica, Colegio de Postgraduados, Chapingo, Edo. México, México.*

NOTEWORTHY PUBLICATIONS OF THE CHRONICA BOTANICA

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———. Supplement to the Ferns of Southern India and British India. Reprint ed. 1979.

CB Rs. 85; LB US $18.50.

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Disjunct Populations of Isoëtes macrospora in Southeastern Tennessee

W. MICHAEL DENNIS*, A. MURRAY EVANS**, and B. EUGENE WOFFORD**

Isoëtes macrospora Dur. is a northern species widely distributed throughout eastern Canada and the northeastern United States west to Minnesota (Pfeiffer, 1922; Wherry, 1961). Recently, populations of this species were found in the Little Tennessee and Hiwassee Rivers of southeastern Tennessee. The only other report of this species from the southeastern United States is that of Svenson and Griscom (1935), who cite it from northern Virginia. This report was accepted by Massey (1944, 1960) and by Harvill, Stevens, and Ware (1977) for the Virginia Flora, but was not mentioned by either Fernald (1950) or by Gleason and Cronquist (1963).

There had been some confusion concerning the county of this Virginia collection. The voucher located in the Brooklyn Botanical Garden Herbarium is labeled "*Isoëtes macrospora* Dur., Shallow Water. Passage Creek. Macrospores Average 650 μ. Frederic Co., VA. L. Griscom and H. K. Svenson 5561, July 2, 1933." Massey (1944) cited the collection as being from Passage Creek in Shenandoah County. This is verified by C. E. Stevens (pers. comm), who corresponded with Svenson, and indicated that Svenson still recalls the locations along Passage Creek as being in Shenandoah County. Recently, this location was examined by A. M. Evans, and plants of *I. macrospora* were found to occur frequently in the shallow, cobble-bottomed pools of the Elizabeth Furnace area.

Both the 1935 and 1978 collections from Passage Creek and the recent collections from the Little Tennessee and Hiwassee Rivers represent significant disjunctions from the glaciated, northern, contiguous range of *I. macrospora* to the unglaciated Ridge and Valley province of Virginia and Tennessee. The Passage Creek population is ca. 300 miles from the northern range, and the Tennessee populations are ca. 450 miles from the Virginia population.

In the Little Tennessee and Hiwassee Rivers, the known populations of *I. macrospora* are limited to sections of river between upstream dams and impounded waters of mainstream reservoirs of the Tennessee River. The habitat is essentially riverine and consists of an alternating series of pool and riffle areas. Water depth is generally shallow (<2 m), but varies depending on releases from upstream dams. These releases also help to maintain a cool water temperature throughout the year (15 to 19° C in July, 1978). Individual plants of *I. macrospora* were found rooted in sand-filled crevices of the rocky, cobble substrate in the moderate- to fast-flowing water of pool areas that are 0.1 to 1.5 m deep. Plants growing in areas of weak currents have slightly erect to recurved leaves which spread from the corm in a symmetrical ring. In areas of strong current, the leaves are prominently recurved and fixed by the downstream current, giving the plants a striking, swept-back aspect.

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Other species found growing in association with *I. macrospora* in the Little Tennessee River include *Podostemum ceratophyllum, Callitriche heterophylla, Potamogeton tennesseensis, P. epihydrus, P. nodosus, Nitella* sp., and *Fontinalis* sp. Perhaps the most notable associate is the rare red alga, *Boldia erythrosiphon* Herndon. This alga was first described in 1964 from Big Walker Creek in Giles County, Virginia (Herndon, 1964) and presently is known from a limited number of localities in the southeastern United States. Interestingly, *B. erythrosiphon* has been found in the three known southeastern localities for *I. macrospora*.

Isoëtes macrospora in Virginia and Tennessee may represent a recent range extension or it may be a disjunct relic of past floras. The widespread distribution of many aquatics has been attributed to long-range dispersal by waterfowl. According to Sculthorpe (1967), *Isoëtes* rhizomes and leaf bases are often eaten by waterfowl, and the disjunct populations of *I. macrospora* in Virginia and Tennessee might have resulted from this dispersal mechanism since migratory waterfowl do frequent the Little Tennessee and Hiwassee Rivers. The distance from the northeastern United States populations of *I. macrospora* (ca. 700 miles) and the requirement of introduction of both mega- and microspores of these heterosporous organisms into a habitat conducive for sporophyte establishment and development are constraints on the hypothesis of recent introduction by waterfowl. The alternative hypothesis is that these disjunct populations may be relics of a past flora in a region that no longer provides generally favorable environmental conditions for this species. This hypothesis is made less likely by the fact that the Tennessee populations occur in two rivers that in recent history have become controlled by upstream dam releases, which have significantly altered the flow and temperature characteristics of the rivers. Surveys of other eastern Tennessee watercourses that offer seemingly suitable habitat for *I. macrospora* have failed thus far to uncover additional populations. The explanation for the occurrence of this northern species in the southeast thus remains an intriguing problem.

Specimens cited:

TENNESSEE: Monroe Co.: Little Tennessee River at Jones Ferry, 26 Jul 1978, *B. E. Wofford & W. M. Dennis 78-133;* Little Tennessee River at Tomatlo Ford, 26 Jul 1978, *B. E. Wofford & W. M. Dennis 78-134;* Little Tennessee River at SW end of Davis Island, 26 Jul 1978, *B. E. Wofford & W. M. Dennis 78-135.* **Polk Co.:** Ca. 1.1 mi from hwy. 411 bridge over Hiwassee River, 27 Jul 1978, *B. E. Wofford & W. M. Dennis 78-167;* Shallow shoals of Hiwassee River at intersection of hwy. 30 and state road 2518, 21 Aug 1978, *B. E. Wofford & A. M. Evans 78-168;* Shallow shoals of Hiwassee River, 1.6 road miles NW of intersection of hwy. 30 and state road 2518, 21 Aug 1978, *B. E. Wofford & A. M. Evans 78-169.* **VIRGINIA: Shenandoah Co.:** Passage Creek, 8 Nov 1978, *A. M. Evans s.n.* Specimens are deposited in the University of Tennessee Herbarium, Knoxville (TENN); duplicates will be distributed at a later date.

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Three New Elaphoglossums from Guatemala

JOHN T. MICKEL*

In preparing a treatment of the Guatemalan species of *Elaphoglossum*, I have found that three of the 37 taxa recognized apparently are unnamed. This is a fairly modest number of novelties; the percentage will be much greater in Mexico, southern Central America, and the Andes from Venezuela to Bolivia. Because of the large number of species in the genus (over 500), the complexities of their taxonomy, the very few regional treatments, and the lack of a usable monograph, the taxonomy of the genus is in chaos and a modern treatment is sorely needed. Efforts to correct this situation are currently underway.

Elaphoglossum apodum var. latum Mickel, var. nov.

A var. *apodo* lamina late nec anguste oblanceolata differt.

Plants epiphytic in wet forests, rarely on ground; rhizome short-creeping, to 6 mm diam.; rhizome scales orange, linear, entire, to 10 mm long; phyllopodia very short; fronds clumped, 25–48 cm long, 4.5–5.7 cm broad; stipe nearly lacking, to 1 cm long, less than 1/10 of the frond length, clothed with orange, spreading, subulate scales and minute, erect, glandular hairs; blade oblanceolate, base cuneate, narrowing very gradually to somewhat abruptly; apex long-acuminate; papyraceous to coriaceous; veins somewhat obscure, free, once- or twice-forked, ca. 1 mm apart, running at a 60–70° angle; hydathodes lacking; blade scales subulate, orange, especially concentrated on the midvein and margin, some scales on the abaxial blade surface, very sparse on the adaxial surface; blade also with minute, erect, glandular hairs; fertile fronds not seen, but ca. ½ as long as the sterile ones (to 13 cm long, 1 cm broad) in var. *apodum*, with linear, orange scales on the abaxial midvein, lacking among the sporangia; spores not seen, but with low ridges in var. *apodum*.

TYPE: Along Rte. 5 between Semococh and La Laguna on road to Chajmayic, Depto. Alta Verapaz, Guatemala, alt. 500 m, 10 May 1942, *Steyermark 46368* (F).

PARATYPES:

GUATEMALA: Alta Verapaz: Vicinity of Cubilquitz, 1.5–2 mi S of Cubilquitz, *Steyermark 44475* (F, US). **Izabal:** Along Río Frío and tributaries, *Steyermark 41554* (F, US). **COSTA RICA: Puntarenas:** Osa Peninsula, *Lloyd 459* (NY), *Seidenschnur 108* and *109* (both NY). **COLOMBIA: Magdalena:** Santa Marta, *H. H. Smith 2688* (NY). **DOMINICAN REPUBLIC: Azua:** San Juan, Loma La Vieja, *Ekman H 13406* (NY, US).

Specimens of this variety are noticeably broader than those of typical *E. apodum*, which is largely West Indian. Although Christensen named Ekman's specimen var. *majus*, he did not publish the name. The new variety resembles somewhat the figure for *E. backhousianum* Moore, which was described from living material from Mexico. Although that species is clearly allied to *E. apodum* and has the frond form of var. *latum*, it has a stouter rhizome (over 2 cm diam.), larger fronds (45–75 cm tall, 7.5–10 cm broad), and darker brown blade scales than does var. *latum*.

Material of *E. apodum* from much of South America is distinctly different from any of the above. The fronds are very long with a narrow base and probably represent yet a different variety or species.

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7187 **Elaphoglossum lanceum Mickel, sp. nov.**

Rhizomata breviter repentia vel suberecta, 1 mm diametro; rhizomatis paleae lineari-lanceolatae castaneae, 7 mm longae; phyllopodia nulla; frondes fasciculati, 9–21(34) cm longi, 1.6–2.4(2.7) cm lati; stipites laminae dimidio brevior usque 2-ies longior; stipitis paleae castaneae patentes subulatae, usque 6 mm longae; laminae steriles tenuissimae lanceolatae vel lineari-lanceolatae, apice acuminatae, basi cuneatae, margine integrae vel crenulatae; nervi conspicui liberi, simplices vel 1-furcati, 2–3 mm inter se distantes, angulo 35–40° abeuntes; hydathodi conspicui; laminae paleae aurantiaco-bruneae subulatae sparsae, 3–5 mm longae; laminae fertiles quam steriles breviores, ca. 16 cm longae, apice acuminatae, basi cuneatae; stipes quam laminam 2–4-ies longior; paleae cum sporangiis immixtae; sporae monoletae, crista intricatim perforata.

TYPE: Southeast shoulder of Cerro Zempoaltepetl, Dto. Mixe, Edo. Oaxaca, Mexico, in rich, wet, pine-oak cloud forest below Patio de Arena, alt. 8200 ft, *Mickel 4900* (NY; isotypes F, UC, US).

PARATYPES:

MEXICO: Oaxaca: Dto. Ixtlán, 65 km N of Ixtlán, 44 km S of Valle Nacional, *Mickel 5165* (NY). **EL SALVADOR: Chalatenango:** Cerro El Pital, *Seiler 161* (NY). **GUATEMALA: Quezaltenango:** Fuentes Georginas: Volcán de Zunil, *Standley 85996* (F); Volcán Zunil opposite Sta. María de Jesús, *Steyermark 35147* (US). **HONDURAS:** Lempira: Montaña de Celaque, *Hazlett 2600* (F).

Epiphytic in wet forests at 1500–2500 m elevation. This species is distinct in the lance-shaped blade, thin texture, scales among the sporangia, and the highly perforated spore crests. Generally the plants are small, but the one large Guatemalan specimen closely resembles *E. buchii* and *E. smithii* of the West Indies. However, the Guatemalan plant has a thinner texture, somewhat more blade scales, and spores with highly fenestrated crests in contrast to the unperforated crests of the West Indian species.

7893 **Elaphoglossum stellatum Mickel, sp. nov.**

Rhizomata breviter repentia, ca. 2 mm diametro; rhizomatis paleae lineari-lanceolatae castaneae integrae, ca. 2 mm longae; phyllopodia conspicua; frondes fasciculati, 6–21 cm longi, 0.4–0.9 cm lati; stipites laminae dimidio breviores, pilis stellatis sparse vestiti; laminae steriles lineares, apice acuminatae, basi cuneatae; nervi vix conspicui liberi, simplices vel 1-furcati, ca. 1 mm inter se distantes, angulo 60–70° abeuntes; hydathodi nulli; laminae dorso pilis stellatis sparse, ventraliter paleis minimis ciliatis vestitae; frondes fertiles quam frondes steriles breviores angustiores longiusque stipitati, usque 10 cm longae, 0.5 cm latae; stipes laminae subaequilongus; lamina pilis stellatis tantum secus costam abaxialem pilosula; sporae monoletae, breviter cristatae.

TYPE: Volcán Tecuamburro, along trail to San Francisco Tecuamburro on summit of volcano, N of Chiquimulilla, Depto. Santa Rosa, Guatemala, *Steyermark 33155* (F; isotype US).

PARATYPE: Río Samalá, below Zunil, Depto. Quezaltenango, Guatemala, *Steyermark 35012* (F).

Terrestrial or epipetric, at 2000–2500 m elevation. *Elaphoglossum stellatum* closely resembles a small, slender specimen of *E. petiolatum*, but can be distinguished from it by the lack of glandular dots on the abaxial surface, the lack of broader scales on the adaxial surface and stipe, and the lighter rhizome scale

color. It is distinguished from *E. pilosum* by the darker rhizome scales, small blade size, and narrow blade. I have seen specimens from South America that are similar to this (small, narrow, with stellate hairs on both blade surfaces), but the specimens lacked names and had somewhat different rhizome scales.

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REVIEW

"THE HOME GARDENER'S BOOK OF FERNS," by John Mickel with Evelyn Fiore. Ridge Press/Holt, Rinehart & Winston, New York. 256 pp. $7.95.—The science of botany, with its multitude of terms, can be a bit formidable to the uninitiated. John Mickel's book does an excellent job of demystification. On the strictly botanical side, it discusses fern morphology, taxonomy, reproduction, and ferns found in various natural habitats. On the horticultural side, it treats the general principles of indoor and outdoor cultivation and deals specifically with reproducing ferns from spores and by vegetative means. Useful lists of fern societies and of public fern displays are provided. Although the text is marred by occasional small errors, these are more than compensated for by the delightfully light-hearted style in which the book is written. The author's enthusiasm about ferns is sure to be contagious and may well set off another round of pteridomania. This book is invaluable for those who are just starting out to grow ferns. Since it touches on so many interesting botanical details which do not usually come to the attention of non-botanists, it also will be useful and interesting to more experienced growers.—*D.B.L.*

The Role of Temperature in the Vegetative Life Cycle of Isoëtes butleri

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Isoëtes butleri Engelm. occurs in Georgia (Boynton, 1902), Tennessee, Missouri, Kansas, Arkansas, Oklahoma (Pfeiffer, 1922; Fernald, 1950), Alabama (Reed, 1965; Kral, 1973), and Kentucky (Baskin & Baskin, 1978).

Throughout its range it is restricted to shallow soils over limestone. In Tennessee, *I. butleri* is restricted to cedar (limestone) glades of the Central Basin and occurs in very shallow soils that range from 5 to 10 cm deep down to bedrock. In the *Isoëtes* habitat, these shallow soils are waterlogged much of the time from late autumn to mid-spring, but frequently are below the wilting coefficient during the remainder of the year (Freeman, 1933). Common associates of *I. butleri* in the Tennessee cedar glades include *Leavenworthia* spp., *Nothoscordum bivalve* (L.) Britt., *Ophioglossum engelmannii* Prantl, *Sporobolus vaginiflorus* (Torr.) Wood, and *Scutellaria parvula* Michx.

In the middle Tennessee cedar glades, leaves of *I. butleri* come above the soil surface in early to mid-March, and micro- and megasporangia develop on the adaxial surfaces of the leaf bases in early to mid-April. Senescence of the leaves begins in mid-May, and by mid-June the leaves as well as the roots are dead. By this time, the spores are mature. The corms remain in an inactive (quiescent) state in the soil until autumn, when growth of new roots and leaves is initiated. Growth of new roots begins in early October and is soon followed by leaf growth. By mid October, roots are 0.5–3 cm long and leaves are 0.5–1.5 cm long. Roots continue to grow until mid November, but there is little additional leaf growth until the following spring, when the leaves emerge above the soil surface.

Thus, the timing of the vegetative life cycle in *I. butleri* is one of the physiological adaptations that allows this drought-intolerant species to persist in its summer-dry, winter-wet habitat. In this study we investigated the role of temperature in regulating the timing of root and leaf growth in the vegetative life cycle of *I. butleri*.

GENERAL METHODS

Corms of *I. butleri* were collected from a cedar glade in Rutherford County, Tennessee on 10 June 1975 and 13 June 1977, after all the leaves and roots were dead. Corms were washed gently and the dead leaf bases (containing intact micro- or megasporangia on the adaxial surfaces) and dried, shriveled roots were removed. Within two days after collection, the corms were placed on a layer of soil 4 cm thick in waxed paper cups (7 cm deep and 8.2 cm in diameter) with drainage holes in the bottoms. Five corms were placed on the layer of soil in each cup. Some of the corms were covered with 2.5 cm of soil; others were not buried. In the latter case, the cups were covered with aluminum foil.

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Studies on root and leaf growth were carried out in an unheated greenhouse in Lexington, Kentucky and/or in temperature-controlled incubators in the laboratory. In the unheated greenhouse, the windows were kept open at all times, and temperatures were near those out-of-doors. Continuous thermograph records of air temperatures in the unheated greenhouse were used to calculate mean daily maximum and minimum temperatures and the number of hours that corms were exposed to "chilling" temperatures between 0.5 and 10° C. From 1 May to 1 September, the soil in which corms were buried was watered to field capacity once each week; during the remainder of the year, it was watered daily except when frozen in winter. These watering regimes were given to approximate the soil moisture conditions that corms would likely be exposed to in the cedar glade habitat.

In the laboratory, four incubators were programmed on 12/12 hr thermoperiods to approximate habitat temperatures from early spring to late autumn: March, 15/6° C; April, 20/10° C; May and June 30/15° C; July and August, 35/20° C; September, 30/15° C; October, 20/10° C; November, 15/6° C (U.S. Dept. Comm., 1965).

For the buried corms, leaves were considered to be emerged when their tips were 5 mm above the soil surface; for the nonburied corms, leaves and roots had to be 5 mm long before they were considered to have initiated growth. Nonburied corms were examined for growth at intervals in a darkroom under a green safe lamp, which consisted of a green fluorescent tube wrapped with a No. 24 dark green sheet of "Cinemoid." Peak intensity of the light as determined with an ISCO Model SR Spectroradiometer was at 550 nm, and essentially all the energy impinging on the corms was between 500 and 600 nm. There was no radiation above 600 nm.

PROCEDURES AND RESULTS

Leaf and root growth under natural temperature regimes.—Fifteen corms collected on 10 June 1975 were kept in the unheated greenhouse until November 1976. During the spring of 1976, each plant went through its normal above-ground annual growth cycle. The leaves emerged in early spring, remained green and healthy until late spring, and then yellowed and died in early summer. On 15 September, 1 and 15 October, and 15 November 1976, the corms were removed from the soil to determine if leaf and root growth had been initiated; after each examination, the corms were reburied. Mean daily maximum and minimum temperatures were calculated for the 15-day period prior to the various dates when the corms were examined.

On 15 September, there were no visible signs of leaf or root growth, although the corms had been kept continuously moist since 1 September. Mean daily maximum and minimum temperatures for the previous 15 days were 31.0 and 17.3° C, respectively. On 1 October, none of the corms had initiated leaf growth, but four of them had initiated root growth. Temperatures for the last 15 days of September were 25.6 and 16.2° C. By 15 October, 10 corms had leaves that were

5–17 mm long and all corms had roots that were 6–30 mm long. For the first 15 days of October, temperatures were 24.4 and 13.6° C. By 15 November, all corms had leaves that were 1–1.5 cm long and roots that were 1–4 cm long. Temperatures during the first half of November were 14.7 and 6.6° C.

Forty corms collected on 10 June 1975 were kept in the unheated greenhouse until 1 October 1976. On this date, 20 corms were transferred to a greenhouse that was heated in the winter, while the other 20 were retained in the nonheated greenhouse. Temperatures in the heated greenhouse ranged mostly from 20 to 30° C during the day and from 15 to 20° C at night. The cups containing the corms were examined for emergent leaves at weekly intervals in both greenhouses until 1 April 1977, and the soil in all cups was kept continuously moist.

In the unheated greenhouse, there was no leaf emergence prior to 16 February 1977. Between 17 and 23 February 1977 (when mean daily maximum and minimum temperatures were 16.2 and 6.4° C, respectively), leaves on eight corms emerged. Between 24 February and 2 March (21.7 and 8.9° C), leaves from seven corms emerged; between 3 and 9 March (17.8 and 7.8° C), leaves from three corms emerged; and between 10 and 16 March (14.8 and 3.0° C), leaves from the remaining two corms emerged. In the heated greenhouse, leaves from only one corm emerged, between 9 and 16 March. When the experiment was terminated on 1 April 1977, the corms in the heated greenhouse were examined and all were still alive.

Initiation of leaf and root growth.—Rates of initiation of leaf and root growth were compared for corms before and after they were exposed to summer temperature and soil moisture regimes in the unheated greenhouse. Eighty corms (16 cups containing 5 corms each) were covered with soil and transferred to the unheated greenhouse, where they remained until 1 September 1977. A second set of 80 corms was not buried, and cups containing them were covered with aluminum foil. Twenty corms (4 cups of 5 corms each) were placed at each of the four alternating temperature regimes. On 1 September, the 80 buried corms in the unheated greenhouse were removed from the soil and placed on a layer of soil in cups which then were covered with aluminum foil. Twenty corms were placed at each temperature. None of the 80 corms kept in the unheated greenhouse during summer showed any signs of root or leaf growth on 1 September. Beginning with incubation at the four thermoperiods, both sets of corms were examined under the green safe light at 5 to 10 day intervals for leaf and root growth, at which time the soil was watered if needed. Observations were made on both groups of corms for 170 days.

There was no root or leaf growth on any corm placed at 30/15 or 35/20° C in either June (June corms) or September (September corms). Corms placed at simulated autumn temperatures (20/10 and 15/6° C) in September initiated root growth faster than did corms placed at the same temperature in June (*Fig. 1*). At 20/10° C, only 12 of the June corms initiated root growth within 170 days, but all 20 of the September corms produced roots within 35 days. At 15/6° C, 100% of the corms placed at this temperature in June and September produced roots; however, it took 120 days for the June corms but only 35 days for the September corms. In

contrast, the rate of initiation of leaf growth was slower for September corms than for June corms (*Fig. 1*). At 20/10° C, eleven of the June corms but only seven of the September corms initiated leaf growth. At 15/6° C, leaves were produced by all of the corms, but growth began sooner for those placed in the incubator in June than in September.

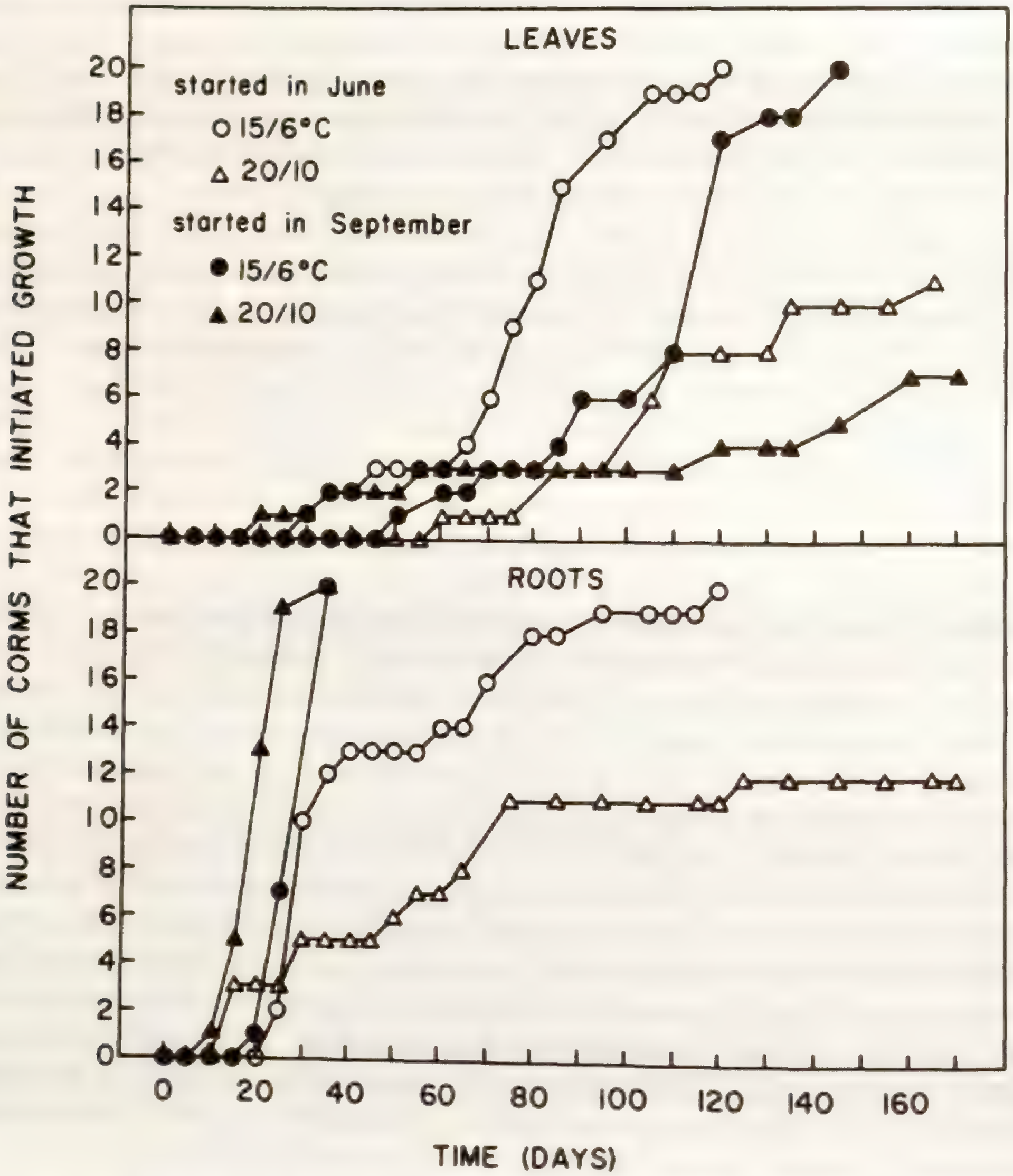

FIG. 1. Growth of leaves and roots of *Isoëtes butleri* before and after the corms were exposed to summer temperature and soil moisture conditions. There was no growth at 30/15 or 35/20° C.

Emergence of leaves from corms collected in June.—Corms collected on 10 June 1975 were buried in cups of soil, and 20 corms were placed at each of the four alternating temperature regimes. The soil was watered regularly, and the cups were examined for emergent leaves at 5- to 10-day intervals for 205 days. No leaves emerged from corms incubated at 30/15 or 35/20° C, and no leaf emergence from corms at 15/6 and 20/10° C occurred until after 80 days (*Fig. 2*). Leaves had

emerged from all 20 corms at 15/6° C after 178 days but from only 13 corms at 20/10° C after 205 days.

Effects of chilling on subsequent leaf emergence.—Corms collected on 10 June 1975 were buried in cups of soil and placed in the unheated greenhouse. On 13 September, 1 October, and 1 December 1975 and on 2 January and 1 February 1976, 20 corms were placed at each of the four thermoperiods, and the cups were examined for emergent leaves at 5 to 10 day intervals for 95 days. After removal to

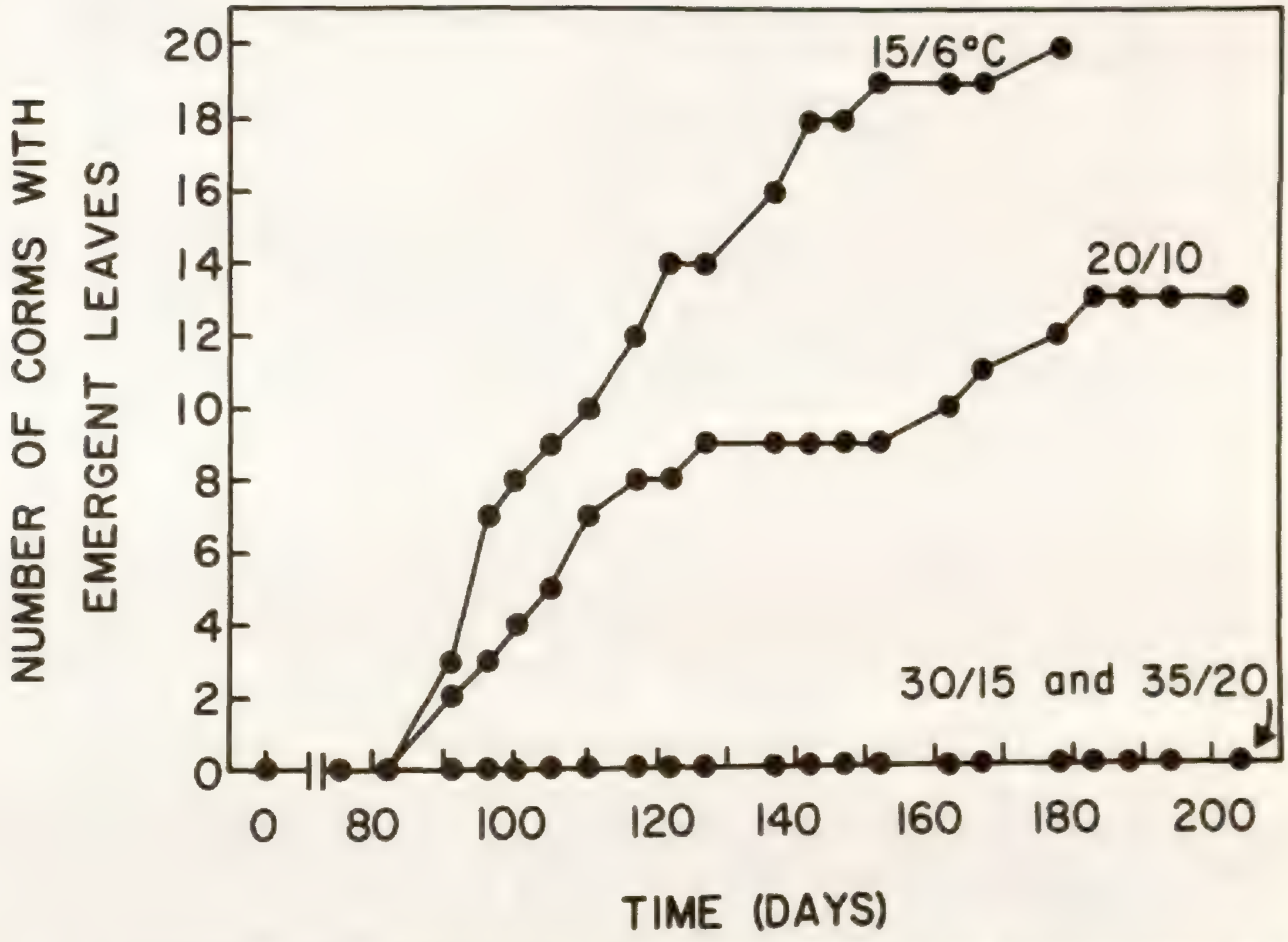

FIG. 2. Emergence of leaves from buried corms of *Isoëtes butleri* placed at the four temperatures on 12 June 1975.

the incubators, the soil in the cups was kept continuously moist. From the thermograph records, we calculated the number of hours that corms in the nonheated greenhouse were exposed to temperatures between 0.5 and 10° C. These temperatures were chosen because they are known to promote vernalization, bud break, and afterripening of seeds (Leopold, 1964; Stokes, 1965; Salisbury & Ross, 1969).

Corms of *I. butleri* transferred to the incubators on 13 September had received 0 h of chilling; on 1 October, 22 h; on 1 December, 486 h; on 2 January, 926 h; and on 1 February, 1,218 h. After 95 days, there was no leaf emergence from corms placed in the incubators in September. However, leaves of corms transferred from the unheated greenhouse to the incubators during autumn and winter exhibited an increase in ability to grow (*Fig. 3*). At 30/15 and 35/20° C, only nine or fewer of the corms had emergent leaves after 95 days, regardless of when they were placed in

the incubators. At 20/10 and 15/6° C, there was an increase in the number of emergent leaves as well as an increase in the rate of emergence. For example, whereas 6 and 11 of the corms placed at 20/10 and 15/6° C, respectively, on 1 October 1975 had emergent leaves after 90 days, all corms placed at these temperatures on 1 February 1976 had emergent leaves after 10 and 30 days, respectively.

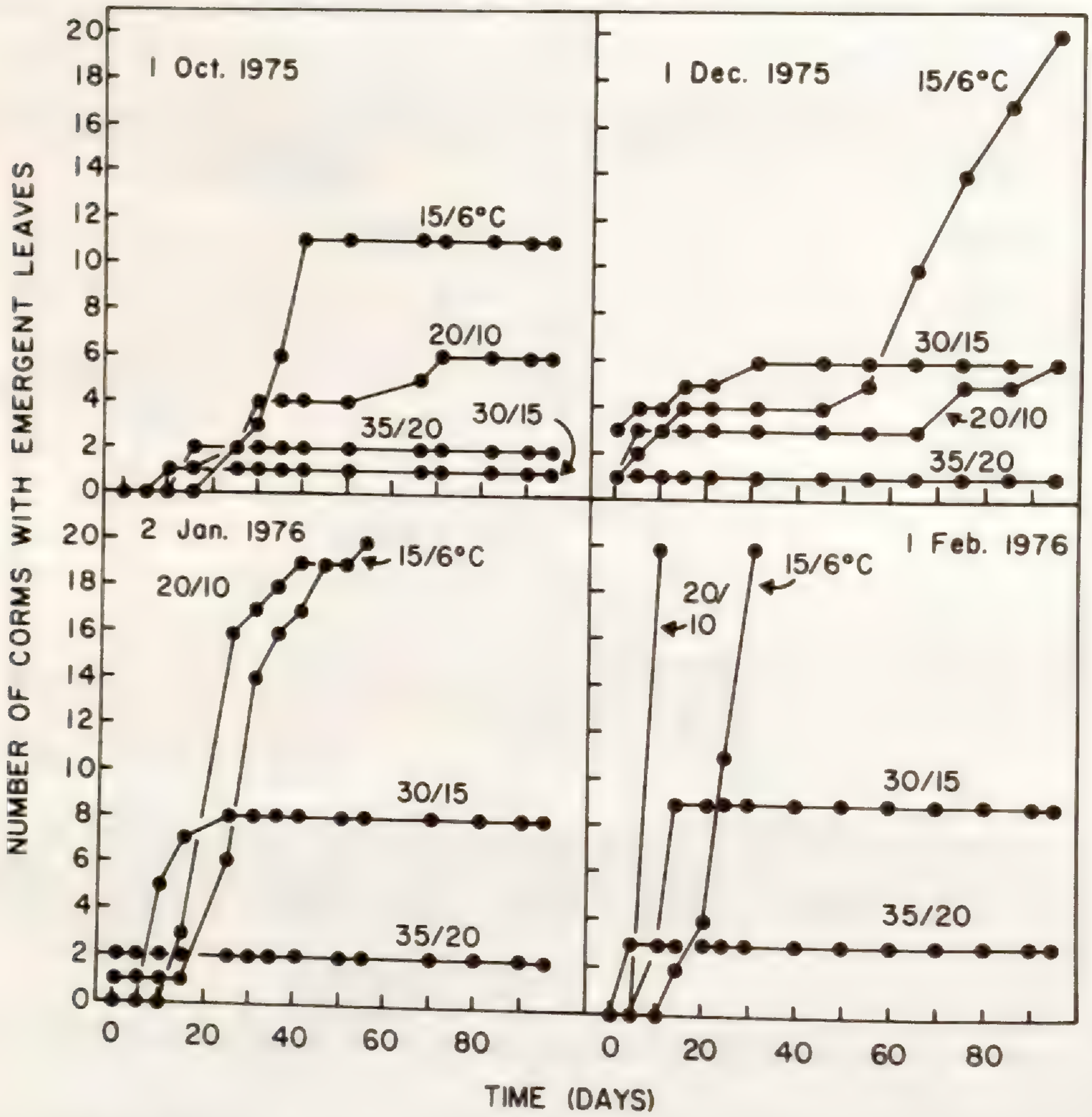

FIG. 3. Emergence of leaves from buried corms of *Isoëtes butleri* placed at the four temperatures on various dates. There was no leaf emergence for corms placed at the four temperatures on 13 September 1975.

DISCUSSION

When the vegetative growth cycle of *I. butleri* ends in June with the senescence of roots and leaves, the corms will produce new leaves and roots if they are incubated at autumn (20/10 and 15/6° C) but not at summer (35/20 and 30/15° C) temperatures (*Figs. 1* and *2*). However, even when corms are incubated at 20/10 or 15/6° C, initiation of leaf and root growth is very slow. At 20/10° C, three corms had roots within 15 days and only one had leaves after 60 days. At 15/6° C, one corm had roots after 25 days and one had leaves after 30 days (*Fig. 1*). At both

20/10 and 15/6° C, the first leaves to emerge from buried corms did so only after 80 days (*Fig. 2*). This low temperature requirement for leaf and root growth in *I. butleri* prevents vegetative growth during the summer because summer habitat temperatures are too high. Thus, although soils in the cedar glade habitat of *I. butleri* may be moist for several days following summer rains, the corms do not produce new leaves and roots. If roots and leaves were formed during brief periods of favorable soil moisture in summer, they would no doubt be killed within a few days after the soil again dried to the wilting coefficient. Occasionally a short period of favorable temperatures for leaf and root growth follows a summer rain (Baskin & Baskin, 1970). However, the slow rate of growth initiation in corms of *I. butleri* in summer prevents the formation of leaves and roots.

Root and leaf growth are delayed until temperatures in the habitat become suitable for growth and completion of the vegetative life cycle. In the nonheated greenhouse, there was no root or leaf growth until after 15 September. From 15 September to 1 October, the mean daily maximum and minimum temperatures were 25.6 and 16.2° C, respectively, and during this time none of the corms produced leaves and only four of them produced roots. Most of the corms initiated root and leaf growth between 1 and 15 October when mean daily maximum and minimum temperatures were 24.4 and 13.6° C, respectively. These temperatures correspond very closely to the mean daily maximum (23° C) and minimum (12° C) air temperatures for October in middle Tennessee (U.S. Dept. Comm., 1965). This explains why root and leaf growth of *I. butleri* in middle Tennessee begins in October. Also, in autumn the soil in the cedar glades stays moist for many days following rains; therefore, soil moisture does not limit growth and survival of new leaves and roots.

Data presented in *Fig. 1* indicate that exposure to summer temperature and soil moisture regimes enhanced the subsequent rate of root, but not leaf, initiation in autumn. In the unheated greenhouse in autumn, corms produced roots earlier than leaves, and roots grew faster than leaves. In the field in autumn, roots grow rapidly and attain much of the potential growth before winter. However, leaf growth is slow and leaves do not emerge from the soil surface until spring.

In plants of *I. butleri*, chilling resulted in a widening of the temperature range, and an increase in rate, of leaf emergence after corms were transferred from the unheated greenhouse to the incubators. With an increase in the number of hours of chilling, there was an increase in the number of corms with emergent leaves and in the rate of leaf emergence at 15/6° C. However, the number of days from 13 September 1975 to 100% leaf emergence did not decrease (*Fig. 3*). Whereas none of the corms placed at 15/6° C in September and only 11 of those placed at this thermoperiod on October had emergent leaves after 90 days, all corms placed at 15/6° C on 1 December, 2 January, and 1 February had emergent leaves after 90, 55, and 30 days, respectively. The number of days (from 13 September) for 100% leaf emergence for corms placed at 15/6° C on 1 December, 2 January, and 1 February was essentially the same, *i.e.*, 168, 165, and 171 days, respectively. At 20/10° C, the number of corms with emergent leaves as well as the rate of leaf emergence increased (*Fig. 3*) and the number of days from 13 September to 100%

leaf emergence decreased. Whereas none of the corms placed at this thermoperiod in October and December had emergent leaves after 90 days, leaves emerged on all corms placed at 20/10° C on 2 January and 1 February in 55 days or less (*Fig. 3*). The number of days (from 13 September) for 100% leaf emergence for corms placed at 20/10° C on 2 January and 1 February was 165 and 141, respectively. At 30/15° C and 35/20° C, leaves emerged on one to nine corms for all dates of transferral except 13 September. This may indicate that chilling widened the temperature requirement for initiation of leaf growth in a small number of plants, but another possible explanation is that growth had been initiated at lower temperatures in the nonheated greenhouse and merely continued at the high thermoperiods in the incubators.

The changes in the physiological responses of the plants caused by chilling during winter allow leaves to emerge in the field in spring at temperatures that, considering time-temperature relationships, were unsuitable for their emergence the previous autumn. In the nonheated greenhouse, leaf growth was initiated in early October, but there was no leaf emergence during autumn although daily temperatures ranged from 15–20° C maximum and 5–10° C minimum. However, leaves on some corms emerged in the spring between 17 and 23 February, when mean daily maximum and minimum temperatures were 16.2 and 6.4° C, respectively, as well as between 24 February and 2 March, when temperatures were 21.7 and 8.9° C, respectively.

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Gametophyte Morphology of the Fern Genus Drynariopsis (Polypodiaceae)[1]

SUBHASH CHANDRA*

As the gametophyte morphology of various fern groups has become better known during the past several decades, it has become increasingly apparent that gametophytes provide dependable morphological criteria for taxonomic and phyletic studies. Bower (1923-28) and Holttum (1949) pointed out that the comparative morphology of fern gametophytes can be of significance in understanding different phyletic groups. Stokey (1951, 1960), Atkinson and Stokey (1964), and Nayar and Kaur (1968, 1969, 1971) discussed the role of fern gametophytes in taxonomic and phyletic studies. According to Nayar and Kaur (1968, 1969), the patterns of spore germination and gametophyte development characterize various taxonomic groups, and so provide dependable data for comparative morphology.

Nayar (1954, 1961, 1965), Nayar and Kachroo (1953), and Bajpai (1964) studied gametophyte morphology of some drynarioid ferns. Until now, no detailed studies of the gametophytes of the monotypic genus *Drynariopsis* have been made, although Nayar (1965) reported that *Drynariopsis* gametophytes show Drynaria-type development. This study of *Drynariopsis heraclea* gametophyte development was made to compare the gametophytes of this primitive genus with those of other drynarioid ferns.

Spores were collected from the fernery of the Natural Science Research Center, University of the Philippines. Gametophytes were raised on sterilized Knop's nutrient agar medium in petri dishes (Nayar, 1962). The cultures were maintained at 24±2° C under 600 ft-c of light from four fluorescent lamps placed horizontally above the culture dishes. All observations on morphology and development of the gametophytes are based on these laboratory cultures. To study cellular structure, the gametophytes were mounted in an acetocarmine solution, which induced partial plasmolysis of the cells and so rendered the cell outlines clear. Drawings were made using a camera lucida.

OBSERVATIONS

The spores of *D. heraclea* are densely granulose, monolete, perineless, plano-convex in lateral view, oblong in polar view, and of medium size. This is confirmed by Nayar and Devi (1964) and by Nayar (1965). Fresh spores contain pale green plastids and prominent, yellowish oil globules. The spores germinate rather slowly; the germ filaments emerge in 3–4 weeks. At germination, the spore cuts off a small, lens-shaped rhizoid initial cell at the proximal pole by a wall formed parallel to the equatorial plane of the spore (the wall perpendicular to the polar axis of the spore). This cell soon forms the first rhizoid (*Fig. 1*) and elongates in the direction of the proximal pole (*Fig. 2*). The distal, daughter gametophytic

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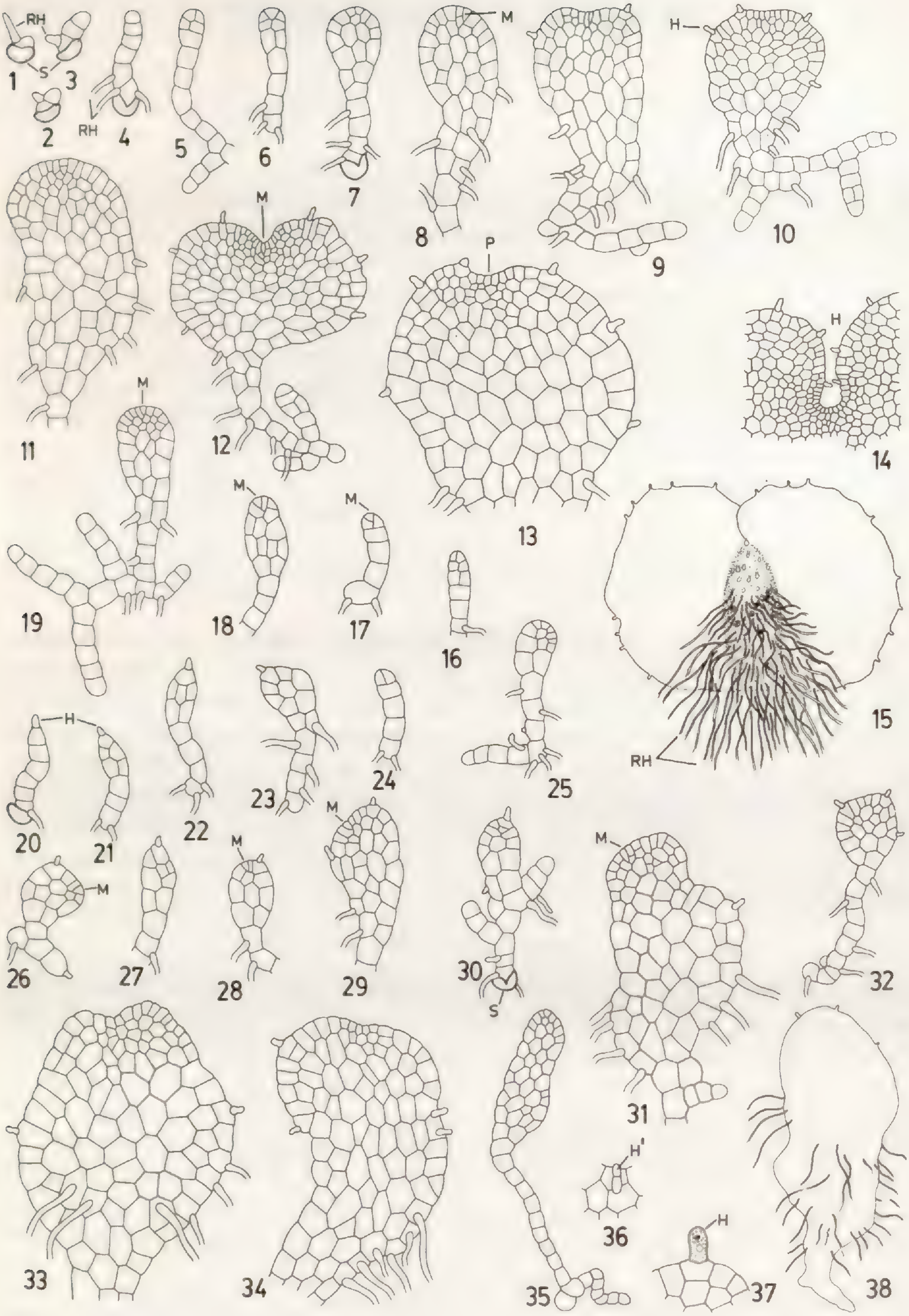
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initial cell enlarges and divides (*Fig. 2*) by a wall perpendicular to the first wall, one that is parallel to the polar axis of the spore. The germ filament elongates along the equatorial plane of the spore (*Figs. 2* and *3)* perpendicular to the first rhizoid. Due to the physical obstruction provided by the spore coat, the germ filament is deflected and the rhizoid is pushed away to one side. The rhizoid, which usually emerges first, is dark brown and devoid of chloroplasts. This is termed Vittaria-type spore germination by Nayar and Kaur (1968, 1971). The germ filament elongates, becomes 4–8 cells long (*Fig. 4*), and is composed of short, stout, barrel-shaped, densely chlorophyllous cells. The basal cell is short, often rather bulbous, and may bear two or more rhizoids. The germ filaments often are branched (*Figs. 5, 9, 10, 12, 19,* and *30*), sometimes profusely so, with the branches developing into separate gametophytes, in contrast to *Pseudodrynaria* (Nayar, 1954) and *Drynaria* (Nayar & Kachroo, 1953), in which branching has been reported to be rare. Development of the gametophytic plate is initiated when the germ filament is 4–8 cells long, and may be either Drynaria-type or Aspidium-type.

Drynaria-type development.—The terminal cell of the germ filament and two or three cells behind it divide transversely and longitudinally to produce a spatulate gametophytic plate (*Figs. 5* and *6*). The plate often becomes 5–10 cells wide and broadly ovate, but is devoid of any organized meristem (*Fig. 7*). Only rarely is an apical cell established early (*Figs. 16–18*), in which case the young gametophyte becomes cordate. For the most part, an obconical apical meristem cell is differentiated later by two oblique divisions of one of the marginal cells at the anterior end of the gametophytic plate (*Fig. 8*). The apical cell undergoes a considerable number of divisions and the gametophyte becomes cordate (*Fig. 12*) before the apical cell is replaced by a multicellular meristem (*Figs. 9–11*). In Drynaria-type development, the establishment of an apical meristematic cell usually is much delayed (*Figs. 16–18*), and the gametophytes usually develop hairs on the margin when the gametophytic plate becomes cordate; the younger gametophytes are naked. In contrast, in *Drynaria rigidula*, an apical meristematic cell is established early, at the second division of the terminal cell, often initiating it (Nayar, 1965).

FIGS. 1–38. Stages in the development of *Drynariopsis heraclea* gametophytes. FIGS. 1–2. Germ papilla. FIGS. 3–4. Germ filament. FIGS. 5–7. Spatulate plate. FIG. 8. Young spatulate gametophyte showing early formation of apical meristematic cell. FIGS. 9–11. Young gametophyte showing establishment of multicellular meristem. FIG. 12. Young cordate gametophyte showing identity of meristematic cell until quite late. FIG. 13. Gametophyte plate showing differentiation of pluricellular meristem. FIG. 14. Apical region of mature gametophyte showing multicellular meristem. FIG. 15. Mature, cordate gametophyte showing formation of antheridia and archegonia. FIGS. 16–18. Early formation of apical meristematic cell. FIG. 19. Branched young gametophyte. FIG. 20. Uniseriate germ filament terminated by papillate hair. FIGS. 21–23. Initiation of plate formation. FIG. 24. Terminal cell of the germ filament with longitudinal division. FIG. 25. Formation of spatulate plate. FIG. 26. Formation of lateral meristematic cell. FIG. 27. Formation of a papillate hair in one of the daughter cells of the terminal cell. FIG. 28. Formation of meristematic cell after hair initiation. FIGS. 29–31. Young gametophytes with slightly asymmetrical meristematic plate. FIGS. 32–35. Ameristic young gametophytes. FIG. 36. Superficial, stalked hair. FIG. 37. Marginal hair. FIG. 38. Young, strap-shaped gametophyte.

As in *Aglaomorpha* (Nayar, 1965), the young gametophytes of *Drynariopsis* often are broader than long, whereas those of *Drynaria* and *Pseudodrynaria* are elongate-oblong at this stage (Nayar, 1965). Soon the apical meristematic cell becomes positioned at the base of the apical notch. It is then replaced by a multicellular meristem (*Fig. 13*) in the usual way, by a transverse wall in the meristematic cell followed by vertical walls in the outer cell.

Under cultural conditions, the gametophytes become distinctly cordate with a multicellular meristem and cluster of rhizoids on the lower surfaces (*Figs. 14* and *15*) about 10–12 weeks after spore germination. The midrib is initiated when the gametophytes are about four months old. The midrib is thin and very conspicuous. The mature gametophytes are cordate, broader than long, grow flat on the substrate, and have a deeply notched apex, as in the other species of drynarioid ferns. The meristem consists of 3–5 elongate cells perpendicular to the surface. The lobes are composed of uniformly thin-walled, densely chlorophyllous, polygonal cells arranged in more or less radiating rows. In contrast to *Merinthosorus* (Bajpai, 1964), the walls of the wings do not possess collenchyma-like thickenings at the corners. As in other drynarioid ferns (Nayar & Kachroo, 1953; Nayar, 1954, 1961, 1965; Bajpai, 1964), the marginal cells of young gametophytes develop unicellular, papillate hairs, which begin to form only after the gametophytes have become distinctly spatulate. The hairs are thin-walled, cylindrical, with a rounded anterior end, and are chlorophyllous. They originate as a protuberance of one of the superficial cells, which elongates and is cut off as a hair. When young, the hairs have a swollen tip with a prominent nucleus surrounded by a few vacuoles on all sides (*Fig. 37*). Simple, club-shaped hairs like those found in *Aglaomorpha, Merinthosorus, Photinopteris*, and *Pseudodrynaria* rarely are found on the surface of *Drynariopsis* gametophytes (*Fig. 36*). Branched, club-shaped, polypodioid hairs as found in other drynarioid ferns (Nayar, 1965) and most other polypodiaceous genera, are absent in *Drynariopsis*.

Drynariopsis gametophytes are attached to the substrate by unicellular, elongate rhizoids. On adult thalloid gametophytes, the rhizoids generally are restricted to the lower surface of the midrib. Rhizoids generally are absent on the wing and margins of cordate-thalloid gametophytes, but in strap-shaped gametophytes, marginal rhizoids are often very frequent and in some cases are characteristically clustered, as on the gametophytes of the Grammitidaceae and some Polypodiaceae (Nayar & Raza, 1970). The rhizoids are soft and nearly hyaline; the rhizoid wall is markedly colored, and often is reddish brown, even at an early developmental stage.

Aspidium-type development.—In contrast to Drynaria-type gametophyte ontogeny, the Aspidium-type is variable in *Drynariopsis* with regard to the sequence of cell divisions. All variations characteristic of Aspidium-type development have been observed in *Drynariopsis*. The most common is that the filament terminates in a unicellular hair (*Fig. 20*). The terminal cell becomes beaked, and the protruding portion is cut off by a transverse wall. Plate formation is initiated by cells behind the terminal cell dividing longitudinally (*Figs. 21*–23). Sometimes the penultimate cell of the germ filament also is sluggish. A broad, usually lopsided

plate is formed by differential cell division behind the sluggish anterior region (*Figs. 23* and *26*). The larger side often bulges out, pushing the terminal hair to one side. All cells except the basal cell may divide longitudinally and take part in plate formation. An obconical meristematic cell is differentiated laterally in the thallus by two oblique divisions in one of the marginal cells on the more expanded side of the plate (*Figs. 23* and *26*). It may be formed either early during plate formation or only after the plate becomes several cells wide. This type of gametophyte development has been reported in *Christiopteris* (Nayar, 1967), *Merinthosorus* (Bajpai, 1964; Nayar, 1965), and *Platycerium* (Bauke, 1878; Orth, 1936; Stokey & Atkinson, 1954). Sometimes the terminal cell of the germ filament, after producing a hair, divides longitudinally. One of the daughter cells then produces a hair (*Fig. 27*). The hair-bearing cell is sluggish, but the other daughter cell actively divides by an oblique division to form a meristematic cell (*Fig. 28*, M). The resulting plate may be slightly asymmetrical (*Figs. 29* and *31*). Marginal, unicellular hairs are produced continuously, whether a meristematic cell is differentiated early or not. In some gametophytes, a plate is initiated prior to hair formation. The terminal cell divides longitudinally (*Fig. 24*), with one daughter cell initiating plate formation. A lateral meristematic cell forms in the plate (*Fig. 25*). The other daughter cell of the terminal cell remains sluggish, and may bear a hair.

The gametophyte grows by the activity of the meristematic cell. Since this cell is lateral, the young gametophyte is lop-sided. The asymmetry is more marked when meristematic cell formation is delayed. Soon the meristematic region becomes notched and apical by unilateral growth (*Fig. 7*). As the gametophytes grow, however, the asymmetry is lost, and the adult thallus is symmetrically cordate (*Fig. 15*). Gametophyte development beyond the establishment of an apical meristematic cell is similar to that in Drynaria-type.

Ameristic gametophytes.—Occasionally ameristic gametophytes occur in culture (*Figs. 32–35*). In such cases, a single, obconical meristematic cell may not be developed at all, and the marginal cells on one side develop a multicellular meristem directly. Ameristic gametophytes also have been reported in *Christiopteris* (Nayar, 1967) and in *Merinthosorus* (Bajpai, 1964).

In some cases, the gametophytes elongate by diffuse growth, become irregular and strap-like with a rounded apex, and often bear profuse marginal rhizoids (*Fig. 38*). No organized meristem is ever differentiated, but the cells constituting the anterior region of the strap-like gametophyte are smaller in size and divide more actively than do the cells in the posterior half. No midrib is produced. The meristem is neither very active nor well defined. All cells of the anterior region exhibit meristematic activity. This type of gametophyte development, termed the Kaulinia-type by Nayar and Kaur (1969, 1971), has been reported in many genera of the Polypodiaceae (Nayar & Kaur, 1969).

Mature gametophytes.—The gametophytes of *D. heraclea* reach maturity about 14–16 weeks after spore germination. The mature gametophytes are cordate and bear sex organs and rhizoids on the lower surface of the midrib. The sex organs are the common type found in the Polypodiaceae (Nayar, 1962). Antheridia are superficial, but on gametophytes growing under crowded conditions, they also

may develop along the gametophyte margins. The antheridia are small, subglobose, and have an undivided opercular cell and a funnel-shaped basal cell. Schlumberger (1911) and Schmelzeisen (1933) have reported the occasional occurrence of a divided cap cell of the antheridium in *Drynariopsis*, but these were not observed in the present study. Archegonia are produced after midrib formation and usually are found mixed with antheridia. The archegonia are the usual type reported in advanced leptosporangiates (Stokey 1951; Nayar, 1962), with a short, slender neck composed of four rows of cells having three or four short cells in each row. The neck is curved away from the apex of the gametophyte, and the neck canal cell is binucleate and swollen toward the tip at maturity.

DISCUSSION

The drynarioid ferns are phyletically a problematic group, and commonly are ascribed a microsorioid ancestry. Among the drynarioid ferns, *Drynariopsis* usually is regarded as the most primitive genus and is considered to be nearest the group's probable ancestor (Copeland, 1947; Holttum, 1947, 1954; Nayar & Devi, 1964; Nayar, 1965).

Drynariopsis exhibits several peculiarities in its gametophyte morphology which are otherwise unknown in the Polypodiaceae. The gametophytes are naked in early stages, and the obconical meristematic cell may be differentiated quite early in development, as in *Microsorium*, or it may be differentiated only after the formation of a spatulate plate, as in *Drynaria* and *Pseudodrynaria* (Nayar, 1954, 1959, 1961, 1965; Nayar & Kachroo, 1953). Besides the common Drynaria-type gametophyte development, which is characteristic of the drynarioid ferns and most of the Polypodiaceae, *Drynariopsis* gametophytes exhibit all the variations characteristic of Aspidium-type development. This is uncommon in the Polypodiaceae, but has been reported in *Merinthosorus drynarioides* (Bajpai, 1964; Nayar, 1965), *Christiopteris* (Nayar, 1967), and *Platycerium* (Bauke, 1878; Orth, 1936; Stokey & Atkinson, 1954). Among ferns of other phyletic lines, this pattern is characteristic of Blechnaceae, Davalliaceae, Dryopteridaceae, and Oleandraceae (Nayar & Kaur, 1969, 1971). However, a strap-shaped gametophyte similar to that of *Drynariopsis* is found in *Christiopteris* and in several microsorioid genera of the Polypodiaceae, e.g., *Colysis, Pleopeltis normalis* (Nayar, 1962), *Dendroglossa* (Nayar, 1963a), *Leptochilus, Paraleptochilus* (Nayar, 1963b), and *Lepisorus* (Nayar & Raza, 1970).

Drynariopsis heraclea is unusual among most of the other drynarioid ferns in its gametophyte development, but shows similarities with *Merinthosorus* in having Aspidium-type development. The possibility of segregating *Merinthosorus* from other drynarioid ferns on the basis of gametophyte morphology, as suggested by Nayar (1965), can be ruled out. Copeland (1947) considered *Merinthosorus* to have evolved from *Microsorium* through *Aglaomorpha meyeniana*, but the similarities in gametophyte development of *Merinthosorus* with those of *Drynariopsis* indicate that *Merinthosorus* is not a derivative of *Aglaomorpha*. And Holttum's contention (1954) that *Merinthosorus* has been derived from *Drynariopsis* is supported.

On the basis of comparative gametophyte morphology, it is likely that *Drynariopsis* is more intimately related to *Merinthosorus* than to any other drynarioid fern, and possibly the latter is derived directly from *Drynariopsis*. The similarities with *Aglaomorpha* in vegetative structures and in fertile fronds presumably are due to parallel evolution.

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A New Species of Selaginella from India

C. B. GENA, T. N. BHARDWAJA and A. K. YADAV*

During a recent survey of pteridophytes of southeastern Rajasthan, India carried out in September 1977, we collected a *Selaginella* which is different from all the known species of this genus. It is being described now as a new species, and is an addition to the 59 species of the genus already recorded from India (Alston, 1945; Panigrahi & Dixit, 1966a, p. 11, 1966b, 1967, 1968; Bole & Almeida, 1977).

Selaginella rajasthanensis Gena, Bhardwaja & Yadav, sp. nov.

Selaginella reticulatam affinis. Caulis prostratus, alterne ramificans; caules laterales non ramificantes praeter basalem tantum qui semel tantum dichotome ramificans. Folia et sporophylla dimorpha et serrata. Folia lateralia elliptica, mediana vero ovata; megasporophylla ventralia, cordata. Megaspora tuberculis rotundis. Microsporophylla dorsalia, oblique lanceolata, costa cum carina adaxiali, margine serrata. Microspora exino laevi et crista sinuata et triradiata.

Stem glabrous, prostrate, bearing rhizophores throughout, 1.5–2.5 cm long, the posterior part (5–7 mm) unbranched, the anterior part bearing alternate branches up to 1.0 cm long, the first one from the base invariably dichotomously branched in mature plants (*Fig. 1*). Leaves serrate, obtuse, dimorphic, the lateral ones (*Fig. 2*) elliptical or oval, 1.5 mm long, 1 mm wide, the median ones (*Fig. 3*) ovate, 1 mm long, 0.5 mm wide. Strobili single at the end of every lateral branch, up to 7 mm long, bearing two ventral rows of megasporangia and 1 to 3 microsporangia or none at all dorsally. Mega- and microsporophylls dissimilar. Megasporophylls cordate, 1.5 mm long, 1 mm wide, serrate, mucronate, borne in the same plane as the lateral leaves. Megaspores light yellow, trilete, spherical, 224–240 μm in diam., with many small, round tubercules on the exine. Microsporophylls obliquely lanceolate, 2 mm long, 1 mm wide, serrate, obtuse with a serrately margined adaxial keel or flap on the midrib (*Fig. 5*), borne in the same plane as the median leaves, with only a few (1 to 3) bearing microsporangia. Microspores brown, trilete, spherical, 38 μm in diam., smooth, the triradiate ridge wavy (*Fig. 6*).

TYPE: Kundakhoh, Shahabad, Kota, Rajasthan, India, growing on an isolated moist rock, Sept 1977, *C. B. Gena & A. K. Yadav* (PUN 2610) (PUN; isotypes: Pteridophyte Biology Lab., Govt. College, Ajmer, India, No. PBL/77/S1–6/28/671, B, BM, CAL, K, LWF, NY, US).

The species is confined to Rajasthan, India and is fertile from September to November. *Selaginella rajasthanensis* resembles most *S. reticulata* (Hook. & Grev.) Spring in general appearance, but it is morphologically quite different from the latter in the following respects: habitat (prostrate vs. erect), branching (uncommon, except for the lowest vs. repeated), rhizophore abundance (common vs. absent), lateral leaf shape (elliptical or oval, serrate, obtuse vs. ovate-oblong, aristate, acuminate), median leaf shape (ovate, serrate, obtuse vs. elliptical, aristate, acuminate), strobilus size (long vs. short), disposition and number of sporangia (megasporangia 12–14, ventral, microsporangia 1–3 or none at all, dorsal vs. megasporangia 1–3, basal, microsporangia 9–12, distal); megasporophyll shape

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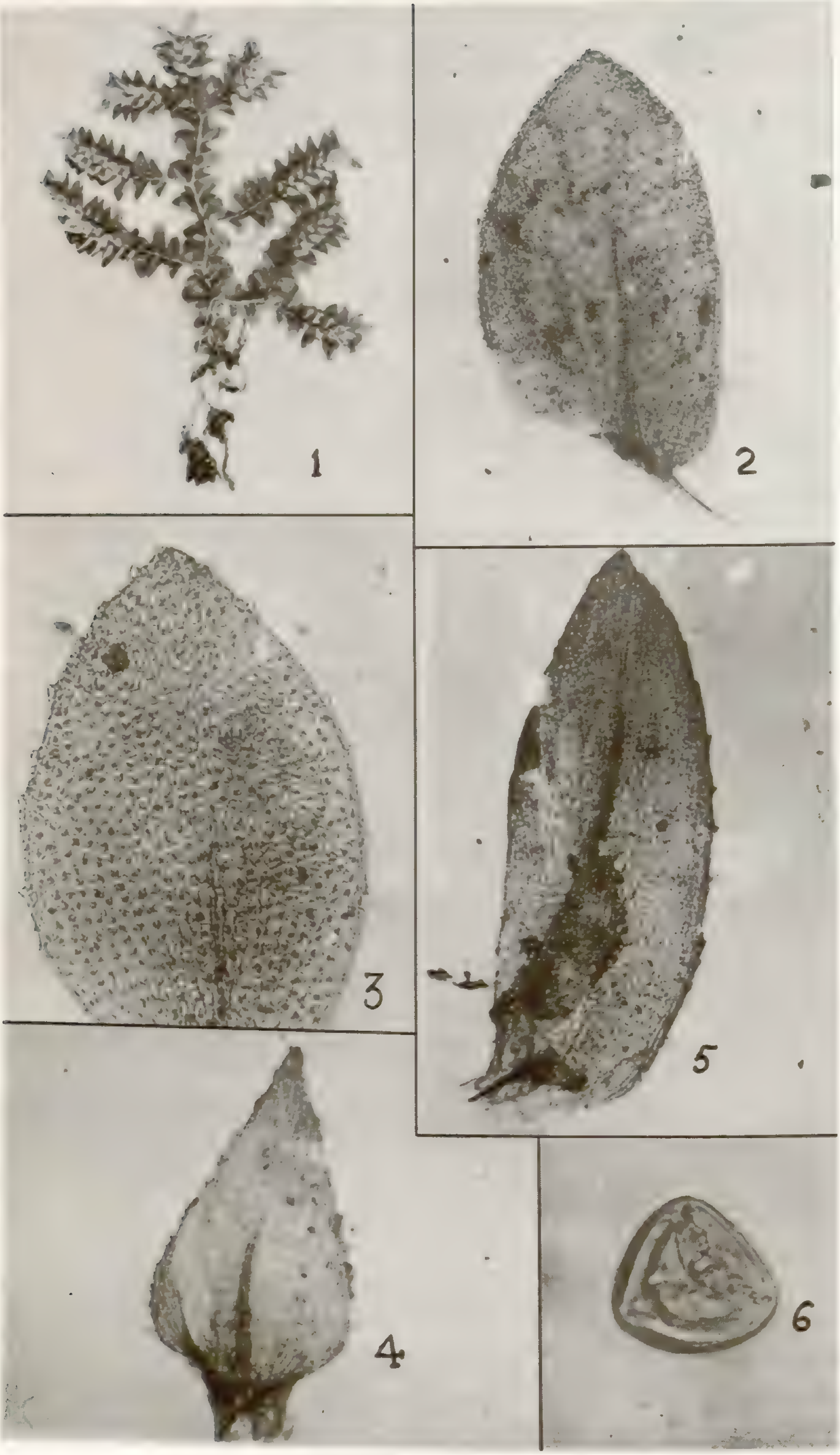

FIGS. 1–6. Details of *S. rajasthanensis* Gena, Bhardwaja and Yadav. FIG. 1. Habit, × 2.5. FIG. 2. Lateral leaf, × 35. FIG. 3. Median leaf, × 85. FIG. 4. Megasporophyll, × 25. FIG. 5. Microsporophyll, × 25. FIG. 6. Microspore, × 430.

(cordate, serrate, mucronate vs. deltoid, aristate, cuspidate); microsporophyll shape (obliquely lanceolate, serrate, obtuse, with an adaxial, serrately margined keel on the midrib vs. lanceolate, aristate, accuminate); megaspore size and ornamentation (larger, the exine with many small, round tubercles vs. smaller, the exine granular); microspore ornamentation (smooth with a wavy triradiate ridge vs. spiny with a straight triradiate ridge).

This new species also differs conspicuously from the recently described *S. tama-montana* Serizawa (1978) from Japan in branching pattern; the latter forms dense mats. The number and disposition of mega- and microsporangia in *S. tama-montana* are rather like those of *S. reticulata*. The strobili of the Japanese species resemble those of *S. reticulata* in the number and disposition of mega- and microsporangia, but sporophyll shape and size is characteristically like that of vegetative leaves in the former. There are significant differences in mega- and microspore size and ornamentation also. These three species may be identified as follows:

1. Plants erect, rooting at the base only, lacking rhizophores. Plants repeatedly branched; leaves and sporophylls aristate; strobilus with 1–3 basal megasporangia and many distal microsporangia; megaspores granular; microspores spiny, the triradiate ridge straight ..... *S. reticulata*
1. Plants prostrate or creeping, with rhizophores present throughout.
   2. Lateral branches not divided, except for the lowermost, which dichotomize only once; leaves and sporophylls serrate; strobili with many ventral megasporangia and only a few, irregularly scattered microsporangia; megaspores with round tubercles; microsporophylls with a serrately margined keel on the midrib; microspores smooth, the triradiate ridge wavy..... *S. rajasthanensis*
   2. Plants frequently branched; leaves and sporophylls serrulate and morphologically similar; strobili with 1–4 basal megasporangia and 6–10 distal microsporangia; megaspores with many reticulations; microspores with uneven tubercles, the triradiate ridge straight ..... *S. tama-montana*

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A SIMPLIFIED NUTRIENT MEDIUM FOR GROWING FERN PROTHALLIA.—Germinating fern spores and culturing prothallia for scientific or educational purposes is usually accomplished by sowing the sterilized spores on Knudson's agar (Bot. Gaz. 79:345-379. 1925; Bot. Gaz. 101:721-758. 1940). The preparation of this medium requires precise weighing of small amounts of essential minerals which are dissolved in water, to which agar is added to solidify the medium. For some time, my laboratory has been successfully using a medium consisting of a solution of 15 gm of agar per liter of water in which is dissolved one commercial nutrient plant tablet (Black Magic Plant Food Tablets, Black Magic, Inc., Box 578-P, Hermosa Beach, CA 90254). The resulting medium provides mineral nutrient yielding fern prothallia in numbers and size equal to those grown on conventional nutrient media requiring precise quantitative mineral additives. —*Norman P. Marengo, Dept. of Biology, C. W. Post College, Long Island University, Greenvale, NY 11548.*

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Page 37, Table 2. For "*FLABELLIFORME*" read "*DIGITATUM*."

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